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**INDIVIDUAL-BASED MODELS ON THE
LANDSCAPE:
APPLICATIONS TO THE EVERGLADES**

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Individual-Based Models on the Landscape: Applications to the Everglades

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Introduction

Theoretical ecology has long been associated with the use of relatively simple mathematical models to describe populations and communities. These models are descendants of the logistic and Lotka–Volterra models, in that they are differential equations (or difference or partial differential equations) and usually contain some sort of nonlinearity, which acts ultimately to limit populations. There have been many elaborations of these models, such as the inclusion of internal age or size structure (e.g., Metz and Diekmann 1988; Caswell 1989) and the inclusion of spatial extent (e.g., Okubo 1980). However, the basic nature of the models remains the same; mathematical models that are simple enough to be written in the compact form of differential or partial differential equations and analyzed. Such models are referred to in general as state variable models. A state variable is used to represent numbers or densities of organisms of a particular population being modeled, or,

alternatively, subpopulations such as particular age or size classes within the population, or subpopulations in particular spatial areas.

During the last three decades, a new modeling approach has developed, individual-based modeling, that is fundamentally different. No state variables are used for population size. Instead, the population is represented as a collection of individuals that are individually modeled (see Huston et al. 1988 and DeAngelis and Gross 1992 for reviews). The focus of the model is on the growth, foraging, survival, reproduction, and other activities of each individual. If one wants to know the total population size, it is necessary only to add up all of the individuals at a given time.

What distinguishes this individual-based modeling approach from the classical models, then, is a different choice of state variables. Individual-based models (IBMs) use variables attached to individuals, individual state variables (ISV), rather than population-level variables to describe the system. The characteristics of each organism (age, size, spatial location, sex, health, social status, experience, knowledge, etc.) constitute the set of variables of the system. Both the number of living individuals and the values of each of their variables can change through time. Such models have long been used to describe a variety of ecological situations. In particular, some of the early work includes models of:

Interactions between plants and other sessile organisms (e.g., Botkin et al. 1972; Maguire and Porter 1977; Ford and Diggle 1981);

Movement of animals (e.g., Rohlf and Davenport 1969, Siniff and Jessen 1969; Skellam 1973; Yano 1978; Kitching 1971);

Transmission of diseases across populations (e.g., Bailey 1967; David et al. 1962);

Population genetics of small populations (e.g., MacCluer 1967; Schull and Levin 1984); and

Animal behaviors; e.g., flocking behaviors in birds, schooling of fish, spacing in response to spatial distribution of food (e.g., Thompson et al. 1974).

Much of the popularity of IBMs results from their reflection of some basic features of real populations: in particular, each individual within a population is unique and differs from others in many biologically important respects. Such differences are easily accommodated in IBMs. For instance:

Individuals are capable of complex behaviors, better described by sets of rules for individuals than by equations at the population level.

Populations of higher trophic-level organisms are often small and hence dominated by stochastic variations. These are not easy to incorporate into population-level equations.

Interactions between organisms are usually highly local spatially, which is difficult to represent by simple equations.

Movement of organisms in complex landscapes is more easily and properly described by sets of rules attached to an individual than by equations (e.g., partial differential equations) at the population level.

The majority of early individual-based modeling involved the modeling of plants, either as single species or mixed stands (e.g., JABOWA, FORET, SORTIE). One of the areas of animal ecology where IBMs have been used extensively is in the simulation of young-of-the-year fish cohorts, where the sizes of individuals in the cohort can differ greatly and strongly influence the recruitment to yearlings (e.g., DeAngelis et al. 1992). Another area is that of the interaction of herbivores with patchy spatial distributions of their plant forage (e.g., Cain 1985).

Currently, IBMs are being combined with GIS maps used to describe species populations, including endangered or rare species, on complex landscapes (e.g., Comiskey et al. 1995; DeAngelis et al. 1998). The approach is currently being applied to model several species of the Everglades under a U.S. Geological Survey Program, Across-Trophic-Level System Simulation (ATLSS). This type of approach will form much of the discussion of this chapter.

An article by Levin et al. (1997) recently outlined some of the potential symbiotic interactions of new computational approaches and mathematical analysis in ecology and other areas of ecosystems science. In doing so, however, the authors made statements that should be more carefully considered. Although the review is a useful one, we feel that it misunderstood the way IBMs are being used. In particular, their comments include:

Because models of this sort may provide an unjustified sense of verisimilitude, it is important to recognize them for what they are; imitations of reality that represent at best individual realizations of complex processes...

The amount of detail in such models cannot be supported in terms of what we can measure and parameterize... The result is that these models produce cartoons that may look like nature but represent no real systems.

Other papers, such as Wennergren et al. (1995), who assessed the use of spatial models in conservation biology including population IBMs, have echoed the view that available data seldom exist to support development of IBMs.

The discussion in the present chapter will be aimed at describing the application of IBMs to species conservation questions, and to some degree, at answering criticisms that individual-based approaches have engendered by presenting examples of IBMs that are currently being used in modeling animal populations in the Everglades.

Individual-Based Modeling in Applied Ecology

Levin et al. (1997) claim that IBMs "may provide an unjustified sense of verisimilitude." This is a somewhat ironical statement in view of the history of mathematical ecology. If the results of simple models such as the Lotka-Volterra predator-prey model had not had an uncanny resemblance to cycles of fish or lynxes and hares, probably little attention would have been paid them. The Lotka-Volterra type model, which has spawned many variations (e.g., Rosenzweig-MacArthur model) was borrowed by theorists from the equations for chemical kinetics. They were used, less because careful observations of the many animal and plant species suggested them, than because they were mathematically tractable and produced interesting behaviors, including cycles that resembled some well-known cycles in nature.

Thus, resemblance between models and observations has always been a main, if sometimes unspoken, argument for the use of those models in ecology. Seldom, if ever, are the analytic models of population ecology derived in the rigorous fashion that a first-year student of physical chemistry or the physics of fluids must reproduce the derivation of chemical kinetics equations, the diffusion equation, or other equations of those fields. Today in mathematical ecology, the same tradition of justifying models based on resemblance (sometimes superficial) of observations continues. For example, many theorists make much of the fact that models of deterministic chaos can produce output that resembles certain time series population data.

IBMs represent a different approach from the classical models of mathematical ecology. The IBM modeler starts from what is known about the actions of individuals under various circumstances. These actions, even if they are very complex, can be represented through computer simulation. The IBMs start with these mechanisms at the level of individuals and attempt to predict the dynamics that should occur at the population level under given circumstances. An IBM can be applied to populations of arbitrarily small size and in highly non-uniform landscapes.

The verisimilitude that IBMs display is not an accidental factor. A basic feature of the approach is that the models predict patterns at a variety of scales of aggregation, from the individuals up to the population level. This is a conceptual advantage, because the models incorporate causal chains leading from the actions of individuals to total population behavior.

In addition, IBMs are amenable to several levels of verification. One type of validation of models is "face validity," where experts in the subject are asked to compare the patterns predicted by the model with their understanding of the system (Rykiel 1996). This type of validation can be applied to IBMs, because they produce output on the detailed distribution of ISV, including distributions in space. This type of validation also tends to be highly Popperian, as these experts invariably try to find fault with the models in comparing

them with what they know of organisms in the field. If the verisimilitude of the models is truly "unjustified," then such a process of validation will detect this.

All models, including very complex IBMs, are certainly abstractions and their usefulness is that they can represent aspects of reality with enough accuracy to help answer questions. But if the verisimilitude that the IBM display extends to making useful predictions, then it is certainly justified.

Levin et al. (1997) further state concerning IBM that "the amount of detail in such models cannot be supported in terms of what we can measure and parameterize...." Wennergren et al. (1995) make the same argument that IBM cannot be supported by data, and that their results are then likely to be erroneous. Wennergren et al. (1995) leave the impression that their negative assessment applies in general to spatially explicit individual behavior models, although their analysis is restricted to a particular dispersal model — a model later published in Ruckelshaus et al. (1997) which was subsequently shown to be in error by two orders of magnitude (see Mooij and DeAngelis 1999).

We are very concerned that notions from papers such as that of Wennergren et al. (1995) and Ruckelshaus et al. (1997), although factually incorrect, are being repeated in the literature. In particular, the view that IBMs are data-hungry and make demands on data accuracy that are impossible to fulfill seems to be widespread. We find this conclusion is of little or no relevance to many of the applications of IBMs to conservation problems. In fact, as will be shown below, IBMs used in applications can be tailored to use spatially explicit empirical data and physiological, behavioral, and natural history information that are typically available from many population and ecosystem studies. Many IBMs are "tactical" models with limited predictive objectives. Data needs for these models are usually parsimonious and can be met with existing or routinely collected data. Other IBMs are more strategic and contain dispersal phases, but without the same degree of sensitivity of model results. Below we consider four examples drawn from our Everglades research.

There are two major components of IBMs as we have used them. The first is a dynamic, spatially explicit description of the landscape. This landscape description includes at least changing water levels at a biologically relevant scale of resolution, 500 × 500 m in this case. Depending on the species modeled, it may also contain vegetation type on the same or finer scale, and a model for changing prey availability.

The second major component is the individual-based description of the species. The models may simulate on this dynamic landscape the entire life cycles of all of the individuals in the population are modeled over many years. Alternatively, the model may simulate the population, or subpopulation, only during the reproductive season. Some models simulate the detailed bioenergetics of individuals, while others may simply simulate demographics and important behaviors, such as movement. This depends on the type of questions being asked and the data available.

Example 1—Cape Sable Seaside Sparrow

The Cape Sable seaside sparrow (*Ammodramus maritima mirabilis*) is an ecologically isolated subspecies of the seaside sparrow (Beecher 1955, Funderburg and Quay 1983; Post and Greenlaw 1994). Its range is restricted to the extreme southern portion of the Florida peninsula almost entirely within the boundaries of the Everglades National Park and Big Cypress National Preserve (Werner 1975, Bass and Kushlan 1982). The sparrow breeds in marl prairies on either side of Shark River Slough. Marl prairies are typified by dense mixed stands of gramminoid species usually below 1 m in height, naturally inundated by fresh water for 2 to 4 months annually. The potential of such habitat for sparrow breeding is dependent upon regimes of fire, hydrology, and catastrophic events (hurricane and frost).

Recent declines in the sparrow population across its entire range, especially the western portion, highlight the need for an effective ecological management strategy. The remaining core of the population occupies approximately 60 to 70 km² in the area adjacent to the southeast of Mahogany Hammock. This subpopulation currently represents 73% of the total population (1996 estimate), and because of the spatial restriction it is seriously at risk to the effects of hurricane or wildfire. Changes to the hydrology of the southern Everglades may also increase the threat of extinction. Increased hydroperiods affect the sparrow in two ways: (a) they can directly shorten the potential breeding season and (b) they can affect them indirectly by causing changes in the vegetation. Recent studies (Nott et al. 1998) show that wetter conditions cause typically short-hydroperiod vegetation (*Muhlenbergia*) to become dominated by sawgrass (*Cladium jamaicense*) and spikerush (*Eleocharis* spp.). This kind of habitat is less suitable for breeding purposes, but remains available for foraging.

The main objective of the model (SIMSPAR) is to investigate the effects of fire and hydrology regimes upon various measurements of the sparrow population. These include lifetime reproductive success of individuals, movement patterns and spatial distributions of the population, and fluctuations in the size and structure of the population and local densities. The model adopts an individual-based, spatially explicit approach. In this model, individual sparrows in the population explore a variable landscape consisting of 500- × 500-m cells. This resolution is ecologically appropriate, considering the minimum territory size, the resolution of many landscape features, and the length of typical "neighborhood" flights.

A set of state variables describes each individual in the population. Individuals differ from one another and respond to both the landscape and to other individuals in the population. The minimum set required to model the observed complexity of the behavior of the sparrow includes spatial location, age, sex, weight, reproductive status, fitness, and associations with others. Individual energetics are ignored, it being assumed that if the habitat of a 500- × 500-m cell is an appropriate habitat, individual sparrows will obtain enough food. The model updates the status of each individual daily according to

ing to movement and behavior rules. The spine of the model is a simple flow of decisions and actions that affect individuals. At each step the model updates the breeding status and tracks associations between individuals.

Each individual (in random order) moves around the landscape according to a simple set of movement rules. These are dependent upon the time of year, the water levels, the status of the individual, the attributes of the cells it encounters, and the attributes of neighboring cells. Important landscape attributes include elevation, vegetation classification, and fire history. Some types of cells represent "reflective" barriers to movement (pine forest, hammock, and open water); other "transparent" cell types allow movement, but do not represent breeding habitat (sawgrass/spikerush marsh). Temporal and spatial patterns in water levels represent the main environmental driving force behind the model. Males will establish territories when they find an unoccupied area within a spatial cell in which water levels have declined to less than about 5 cm. Nests are built at about 15 cm above ground level and will be abandoned if flooded. A pair of sparrows requires about 45 days to raise a brood.

A set of behavioral rules mimics observed interactions between individuals. The outcome probability of encounters between individuals is dependent upon their relative status. This determines the next movement of each individual, and updates the associations between individuals. For instance, early in the breeding season two neighboring males may fight over the borders of their respective territories. After this stage they reinforce the limits of their territories by countersinging and other less physical behavior. However, males chase neighboring males more often when they are caring for nestlings (Lockwood et al. 1997). Fighting may also be triggered when a bachelor male or juvenile enters an established territory. Normally, the resident male will drive off the intruder.

The direction of unpaired female movements is influenced by the proximity of territorial males. This simulates the fact that male song can be heard (at least by humans) from several hundred meters away. Subsequent encounters between unpaired territorial males and unpaired females may result in successful mating. As breeding activity diminishes the sparrows form small cohesive groups, and associations between individuals become more complex.

SIMSPAR has been used extensively as part of the ATLSS Program to evaluate the impact of hydrological plans on the demographics of the Cape Sable seaside sparrow. These evaluations used a 31-year planning horizon and provided relative assessments of one plan versus another in its impacts on sparrow breeding success, population size, and spatial distribution.

Although this model is simpler than many that will be used in ecosystem management planning, some generalizations can be made from this on the appropriate approach to modeling. First, the model of an ecological system starts with the basic elements, individuals on a dynamically changing landscape. Second, it uses the simplest set of species characteristics essential to the problem of interest: timing of mating behavior and nest initiation, and effects of water levels on initiation and continuation of nesting. Third, it uses relevant

information on the primary environmental factor, water level (daily changes in water level in each 500×500 m spatial cell). This model is fairly representative of many of the IBMs used in assessment. It belies the claim of Levin et al. (1997) that "the amount of detail in such models cannot be supported in terms of what we can measure and parameterize..." The IBMs approach is highly advantageous for using the type of data available for specific systems and can be quite parsimonious in its data needs.

Example 2—Wading Birds

A second example is a simulation to evaluate the success of foraging animals over short time periods (as opposed to long time period population models), for which pertinent behavioral information may be the most easily available. Wolff used such a tactical approach for a landscape-level IBM simulating the wood stork (*Mycteria americana*), a wading bird listed as endangered in the U.S. (Wolff 1994; Fleming et al. 1994). This model attempts to predict the breeding success of a wood stork colony under different environmental conditions in the Everglades by simulating the immediate prenesting and nesting periods of these colonial wading birds. Breeding success is a crucial component of the overall health of this population and may be a primary determinant of the viability of the population. It is also readily observable. The individual wood stork forages over a large, heterogeneous landscape, and its success in raising its nestlings depends on the spatial and temporal availability of its food (mainly fish and aquatic macroinvertebrates), which is a strong function of changing water levels within foraging distance of the colony of the individual bird. Wolff developed a model incorporating wading bird bioenergetics and behavioral rules derived from the literature and from discussions with experts on the species. The model makes detailed predictions, based on the foraging capabilities of the wood stork of how different landscape topographies and water management scenarios would alter wood stork reproductive success (Wolff 1994; Fleming et al. 1994). Because reasonably good information is available for all important processes, Wolff's model can make highly specific predictions that should be useful in comparing various possible conservation strategies.

Example 3—Florida Panther/White-Tailed Deer Interaction

The underlying assumption in the model of Wennergren et al. (1995) is a "patch view" of the world, with only two states for any particular patch (suitable and unsuitable), and a view that dispersal mortality is a significant fraction of overall mortality. While such a caricature may be reasonable for some species and habitats, there are many cases for which a spatial continuum of continually varying resources is more appropriate, and in which there is no critical dispersal phase leading to high mortality. This is the case for the third example is an individual-based, spatially explicit model of interacting white-

tailed deer and Florida panther populations in South Florida (SIMPDEL, Comiskey et al. 1995).

SIMPDEL (spatially-explicit individual-based simulation model of the Florida panther and white-tailed deer in the Everglades and Big Cypress) includes four major components, hydrology, vegetation, deer, and panthers, and is designed to provide a detailed assessment of how spatial changes in water level affect growth, reproduction, foraging, mating, and predation across South Florida (Comiskey et al. 1998; Abbott et al. 1997; Mellott et al. 1998). It makes use of detailed physiological and behavioral information for the two species, as well as information on vegetative growth under varying hydrologic conditions. Panther movement patterns are derived from radio collar information, and the movements predicted by the model can be explicitly compared to historical movements of individual animals. Data on mortality for deer and panthers have been collected over the past several decades. This allows for realistic levels and causes of mortality to be included, such as deer stranding on high elevation sites during high water conditions, which can lead to starvation, and panther deaths due to intraspecific aggression.

The white-tailed deer, like other large herbivores, forages over a heterogeneous landscape of many localized areas containing resource densities ranging from zero to high levels. This is a case for which a spatial continuum of continually varying resources is more appropriate than the two-state model of Wennergren et al. (1995). This is true as well for large carnivores for which the inherent prey resource, though possibly patchy, moves about in space continually. Such organisms may also have a memory, and elaborate territorial behaviors, which may easily obviate the dispersal error propagation problem the authors infer from their simplified world view. In a continuously distributed resource world, our intuition and model simulations to date do not indicate the strong sensitivity of individual success to small changes in individual movement behavior that the authors claim exists. In this model and others like it (e.g., Hyman et al. 1991; Turner et al. 1995), modeling of populations over many generations seems reasonable.

The above examples illustrate that spatially explicit IBM is actually much broader and more flexible than one would gather from reading the discussion of dispersal in Wennergren et al. (1995). This approach has been developed as a way of taking into account physiological and behavioral processes that could be essential, or at least play a role, in situations involving one or more populations, but that can not be incorporated into the traditional models of population ecology; e.g., small sets of difference or differential equations. The approach makes use of information at the individual organism level that has long been the subject matter of physiological and behavioral ecologists. One can incorporate rules of behavior that are difficult to reduce to simple mathematics.

These examples of IBMs also undermine the pessimistic inference by Wennergren et al. (1995) that IBMs are disadvantageous because they are "data hungry," and the similar criticisms of Levin et al. (1997). For many species of

interest, there is a great amount of empirical information already available on behavior and bioenergetics. Rather than being a liability, individual behavior models increase the relevance of behavioral ecology to population ecology. These models are a means for utilizing large amounts of data already collected, often at great cost, at the individual level. The combining of behavioral and physiological information into individual behavior models also helps to reveal gaps in existing data that could stimulate more focused and useful field studies. In many cases, IBMs can already be applied with little or no further demands on data collection, and they can contribute predictive power to conservation problems in a number of ways.

Contrary to the claim by Levin et al. (1997) that IBMs "... represent no real systems," IBMs are clearly being used to address specific questions of specific systems. We believe that for the goal of prediction for specific conservation issues there is no alternative to such detailed site-specific ecological modeling. Abstract ecological models seem to offer little concrete predictive power to conservation ecology. As Shrader-Frechette and McCoy (1993) point out, "... although ecologists' mathematical models may have substantial heuristic power, it may be unrealistic to think that they will ever develop into general laws that are universally applicable and able to provide precise predictions for environmental applications." Generalizations stemming from simple, abstract models are vague, often contradictory, and hotly debated by ecologists (Shrader-Frechette and McCoy 1993). The alleged "shakiness of (detailed) spatial models as a foundation for specific conservation recommendations" cited by Wennergren et al. (1995) should be compared with the questionable foundation for prediction provided by more abstract models.

IBMs and Ecological Theory

The individual-based approach also provides an avenue for important theoretical progress in ecology. E. O. Wilson (1975) forecast that behavioral ecology and population ecology would be tightly interfaced by the end of the 20th century. Much of this interfacing, if it is to occur, will be accomplished through the extension of population models to incorporate the behavior and energetics of individual organisms in a realistic way. This will pave the way towards theory reduction, or interpreting the "higher-level phenomena" of population dynamics in terms of "lower-level processes" or mechanisms at the individual level (Shrader-Frechette and McCoy 1993). Because theory reduction is one of the ultimate goals of science, and because theory reduction is a form of simplification in science, the basing of population modeling on individual behavior is a step toward the consolidation and simplification of ecological theory.

In addition to the impressive empirical work at the individual organism level by behavioral ecologists, there is also highly developed relevant theory

at the individual level, such as foraging theory (Stephens and Krebs 1986). If this individual-level theory is judiciously used to help predict energy and time constraints on foraging, the linkages between individual-level theory and population-level theory can be developed.

We disagree with the statement of Levin et al. (1997) that "... only aggregate statistical properties can be reliably predicted, typically over broad spatial and temporal scales." In fact, one can reliably predict that patterns of activity and interaction of individual organisms will lie within bounds imposed by physiological and behavioral constraints at all spatial and temporal scales. This is the whole basis for the use of foraging models and other models of individual animals subject to time and energy constraints.

The wood stork model of Wolff (1994) and white-tailed deer-Florida panther model of Comiskey et al. (1995) are examples of how knowledge of the physiological and behavioral constraints on individuals can be used in models to predict the population-level effects, illustrating theory reduction. Therefore, these models are important not only from an applied viewpoint, but also from a theoretical one. The spatial picture provided by IBMs elucidate the connections between individual-level mechanisms and higher-level patterns, and help to ensure that we are not deceived by superficial resemblances of models to reality at any level of aggregation.

We believe that the development and study of models of this type are essential for understanding the connections between adaptations at the individual level and the dynamics of populations and communities. Models such as the logistic, Lotka-Volterra, McKendrick-von Foerster and the other analytic models of mathematical ecology have served their purposes, but are unable to deal with the fundamental fact that ecological systems are made up of unique individuals in highly complex environments. The desire to produce a unified, parsimonious theory built on the types of equations that have proven so successful in the physical sciences is understandable. But the use of simple analogs of these equations in ecology will go only so far in that direction.

The kinetic equations of physical chemistry, which many models of mathematical ecology emulate, are valid in the domains in which they are used because (1) the basic units (atoms, molecules, or ions) are identical, (2) they are invariant particles that are, for all practical purposes, unchanging, (3) the numbers of these basic units approximate 10^{23} , and (4) approximate spatial uniformity holds in the systems being modeled. None of these facts of physical systems holds for biological populations in natural settings. Each individual in a population differs from all others. A species is not invariant, but has adapted, through natural selection, to its environment. Thus, it is completely dependent on the environment in which it has evolved, down to fine-scale details. Populations of interest are frequently very small, and nearly all populations are too small to justify continuous state variable models such as partial differential equations for describing populations in space.

The hope of many ecological theorists has long been that important ecological problems could be addressed with a few assumptions framed in simple

models. This has fostered a style in traditional theoretical ecology of relying on abstract models with no more than a few equations and, therefore, only a few parameters. The use of abstract models has been a successful strategy for generating interesting general theory. But the deficiencies of abstract models are becoming more obvious even in the domain of general theory, because these models cannot incorporate in a realistic way the behavior of organisms, without which ecological theory has only limited applicability to real populations.

For progress to be made in conservation biology and other applied areas of ecology, the traditional abstract models of theoretical ecology are even less likely by themselves to be a successful strategy. The objective of models applied to practical problems should be to bring to bear as much pertinent information on a problem as necessary. This will often include the use of detailed models, when they are supported by data. This is nothing new in the environmental sciences. Environmental scientists and engineers routinely use models with thousands of equations (in hydrology, for example). Wennergren et al. (1995, p. 349), refer to even a modest set of equations for age and spatial structure as "unwieldy," though models of much greater size are hardly termed unwieldy by modelers in other sciences. Whereas Wennergren et al. (1995) state concerning spatially explicit individual behavior models that "...the realism' of these models is no guarantee of their usefulness," we believe that a high degree of realism is at the very least a prerequisite in any model for it to be useful in conservation ecology. If theoretical ecology is to play a role in conservation and achieve the status of a predictive science, a wide variety of modeling approaches is needed.

While we have focused in this chapter on IBM approaches and argued for their utility in analyzing site-specific environmental problems, the program that these models are a part of takes a broad view of potentially useful approaches. The ATLSS Program (see <http://atlss.org/>) explicitly includes a multimodeling framework in which a mixture of different modeling approaches are applied. In addition to the IBMs discussed here, ATLSS models include: spatially explicit species index models that produce single values for each spatial cell once a year to summarize the effects of within-year dynamics on the foraging and breeding conditions at a site (Curnutt et al. 1999); and spatially explicit, structured population models that follow the size distribution of populations within each spatial cell (Gaff et al. 1999)

The mixture of approaches in ATLSS allows specification of the organismal, spatial, and temporal level of detail appropriate for the trophic level under consideration and can also account for the limitations imposed by available data. Multiple approaches allow somewhat independent assessments of the impacts of alternative management plans to be made, using different models. As one example of this, predictions of the wading bird model described above may be compared to index models for wading bird breeding potential, which are estimated yearly, and to results from a size-structured fish model that allows within-year tracking of the amount of fish available to wading birds. Conformity of the assessments of management plans drawn

from separate models strengthens the utility of such assessments for management. Additionally, using a mixture of models offers the possibility of teasing apart the relative contribution of additional model complexity to the overall assessment.

