united nations
educational, scientific
and cultural
organization

international atomic
energy agency

the
abdus salam
international centre for theoretical physics

H4.SMR/1202-14

"Fifth Course on Mathematical Ecology
including and introduction to Ecological Economics"

28 February - 24 March 2000

LANDSCAPE MODELING FOR EVERGLADES ECOSYSTEM RESTORATION

Louis J. Gross

Institute for Environmental Modeling,
Dept. of Ecology and Evolutionary Biology
University of Tennessee,
U.S.A.

Ecosystems (1998) 1: 64–75

ECOSYSTEMS

Landscape Modeling for Everglades Ecosystem Restoration

Donald L. DeAngelis,[1]* Louis J. Gross,[2] Michael A. Huston,[2]
Wilfried F. Wolff,[3] D. Martin Fleming,[4] E. Jane Comiskey,[5]
and Scott M. Sylvester[5]

[1]US Geological Survey/Biological Resources Division, Department of Biology, University of Miami, Coral Gables, Florida 33124; [2]Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996; [3]Department of Biology, University of Miami, Coral Gables, Florida 33124; [4]US Geological Survey, Biological Resources Division, Everglades National Park, Homestead, Florida 33133; and [5]Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996, USA

ABSTRACT

A major environmental restoration effort is under way that will affect the Everglades and its neighboring ecosystems in southern Florida. Ecosystem and population-level modeling is being used to help in the planning and evaluation of this restoration. The specific objective of one of these modeling approaches, the Across Trophic Level System Simulation (ATLSS), is to predict the responses of a suite of higher trophic level species to several proposed alterations in Everglades hydrology. These include several species of wading birds, the snail kite, Cape Sable seaside sparrow, Florida panther, white-tailed deer, American alligator, and American crocodile. ATLSS is an ecosystem landscape-modeling approach and uses Geographic Information System (GIS) vegetation data and existing hydrology models for South Florida to provide the basic landscape for these species. A method of pseudotopography provides estimates of water depths through time at 28 × 28-m resolution across the landscape of southern Florida. Hydrologic model output drives models of habitat and prey availability for the higher trophic level species. Spatially explicit, individual-based computer models simulate these species. ATLSS simulations can compare the landscape dynamic spatial pattern of the species resulting from different proposed water management strategies. Here we compare the predicted effects of one possible change in water management in South Florida with the base case of no change. Preliminary model results predict substantial differences between these alternatives in some biotic spatial patterns.

Key words: Everglades; landscape model; ecosystem model; indicator species; wetlands; computer simulation.

INTRODUCTION

A very large effort has begun toward restoring the Everglades and other ecosystems in southern Florida. The hydrology of much of the system, from the headwaters in the Kissimmee River southward to the northern and eastern borders of Everglades National Park, is being reengineered, and land is being purchased to provide areas of water storage and buffer zones between natural areas and the growing urban areas around them. Some of these actions are under way, whereas others are still in the planning stage (SFWMD 1992). Planners need to know which of these options will be most effective in restoring a sustainable ecosystem.

To make useful predictions of the ecological consequences of a given restoration plan, a framework is necessary that can synthesize what is known about the past and present of southern Florida's ecosystems and project their future under changing circumstances. Potentially, modeling can play this role and enable us to predict the outcome of various management scenarios. This report describes a par-

---

Received 30 April 1997; accepted 16 September 1997.
*Corresponding author.

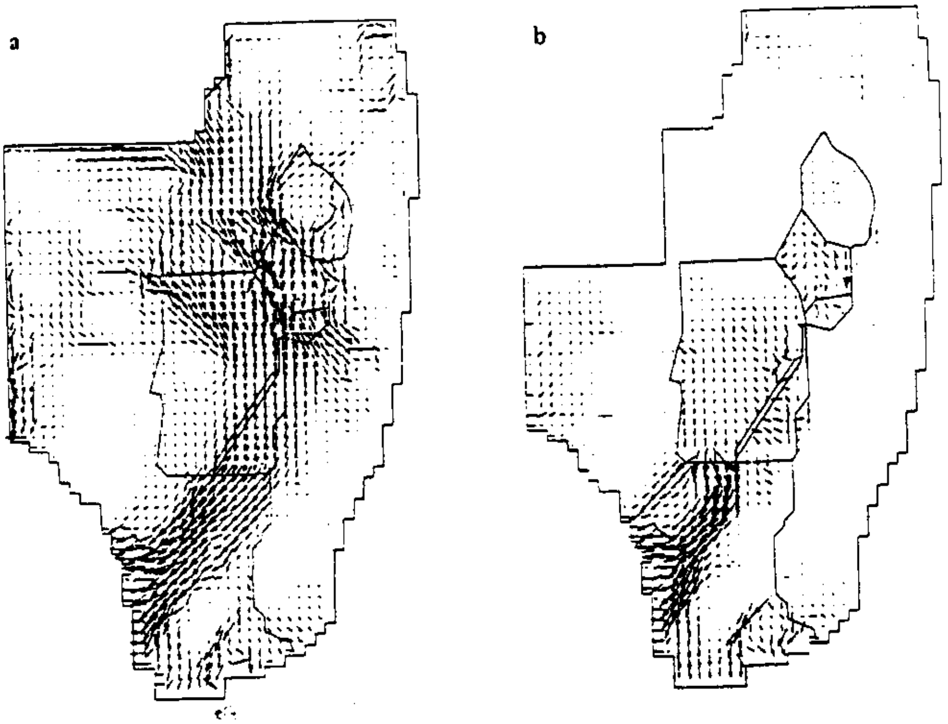


Figure 1. Patterns of overland water flow for a particular date (30 September 1988), computed by models of the (a) natural and (b) managed South Florida system (Fennema and others 1994), showing the decreases in flow in the managed system. The major route of water flow is the Shark River Slough. The Water Conservation Areas (WCAs) north of Everglades National Park are outlined, and the approximate eastern boundary of the park is shown.

ticular modeling approach that will be used to provide assessments of the ecological consequences of proposed restoration plans. We discuss some initial simulation results.

THE EVERGLADES ECOSYSTEM AND HUMAN INFLUENCES

Wetland ecosystems cover much of southern Florida. The Everglades is a huge freshwater marsh stretching from Lake Okeechobee south toward Florida Bay and the Gulf of Mexico. This freshwater marsh is, however, only part of the complex of ecosystems of the region, which include the cypress swamps to the west in Big Cypress Swamp, mangrove swamps and tidal creeks to the south and southwest of the Everglades, pinelands, and tree islands.

A prevailing abiotic influence on this landscape is water, which rises and falls in response to the seasonal pattern of rainfall. Water flows from Lake Okeechobee toward the south and southwest (see Figure 1a, which shows the patterns of flow in the natural system), but the tilt of the land is so slight that horizontal movement of water is very slow and local precipitation, as moderated by human control systems, is usually the greatest influence on water level. The average annual period of inundation of a particular area of land is called its hydroperiod. Most parts of the Everglades landscape are dry for some portion of the year, though some parts remain continuously flooded except during the most severe droughts. Fire, freezing, and severe storms are other physical factors that play a role in shaping the biota of this landscape.

The Everglades food web is based on algae and detritus (Browder and others 1994). The freshwater marshes of the Everglades are relatively oligotrophic and not highly productive, averaging only about 150 g m^{-2} $year^{-1}$ in wet prairie areas (Duever and others 1986). However, because of the flooding and drying cycle, with rapid decomposition during the dry period, much of the primary production is transferred into the detrital food chain, to fish and aquatic macroinvertebrates, and to higher trophic levels, such as wading birds.

A full understanding of the way energy is channeled up the food chain requires a landscape view. The relatively flat topography of the Everglades and the seasonality of rainfall together create a distinctive feature of the natural hydrology: a pattern of sheet flow across the landscape. Before the changes caused by drainage described below, a broad area (up to 90 km wide) was inundated up to a depth of 0.5 m during part of the year, creating a continuous spectrum of hydroperiods, from the long hydroperiods of the deeper central slough areas to the short hydroperiods of the higher elevation "peripheral" wetlands (Fennema and others 1994). During flooding, populations of small fish, crayfish, and so on, are nourished by detritus and seasonal algal growth and, being relatively protected in the shallow marshes from large, predatory fish, reach large numbers. During the dry period, the fish are concentrated into pools and depressions by the receding waters.

Wading birds are beneficiaries of this concentration of prey, which provides sufficient food for their nestlings. The short-hydroperiod wetlands dry out early in the dry season, and the longer-hydroperiod wetlands dry out progressively later. In this way, a "drying front" moves across the landscape from higher to lower elevations. The wading birds, foraging from fixed colonies, follow the drying front, which can provide a relatively constant supply of food for the birds and their nestlings.

Human intervention in this natural hydrology of central and southern Florida began early in the 20th century. In response to hurricanes and the consequent flooding of huge areas and losses of human life and property, the US Army Corps of Engineers built levees, canals, pumping stations, and water-control structures, separating what was left of the Everglades from the rapidly growing urban areas to the east and dividing them into several basins (Light and Dineen 1994). The northern Everglades were partitioned into a series of Water Conservation Areas (WCAs) and the Everglades Agricultural Area immediately south of Lake Okeechobee (Figure 1b), which includes 470,000 acres of sugar cane. The southern Everglades, which acquired national park status in 1947, received water from the southernmost of these WCAs, through control structures at several locations.

The development of the water-control structures greatly altered the Everglades landscape. There has been a major reduction in the amount of water flowing to the downstream Everglades. The inflow from the WCAs to Shark River Slough was estimated by a hydrologic model to be 35% lower in the regulated (postdrainage) system than in the predrainage ("natural Everglades") (Fennema and others 1994). The model of Fennema and others also showed that on average there is a much more rapid drop in flow after the end of the wet season in the postdrainage system. In addition, there are sharp peaks in water deliveries due to pulsed releases through the water-control structures. The net effect of these changes is that in the postdrainage system there is (a) a loss of uninterrupted sheet flow, (b) pronounced fluctuations in water levels, and (c) higher frequency of major drydown events. In addition, because of land-use changes, such as drainage for agriculture, there has been a disproportionate loss of high-elevation short-hydroperiod wetlands.

Concomitant changes in the key wildlife have occurred. Since the 1940s, it has been estimated that there has been a more than 90% reduction in the total wading bird nesting population in the southern Everglades (Ogden 1994). The population of Cape Sable seaside sparrows has declined drastically since the mid-1950s (Lodge 1994).

The life cycles of many other species besides the wading birds are also attuned to the natural hydrology of the system. Under natural conditions, the sheet flow of water was relatively continuous during the wet season. The changes in water depth were gradual and major drydowns of the system were rare. The success in survival and reproduction of many species depends on a reasonable regularity in the rise and fall of water level through the year. For example, rapid fluctuations in water level can affect reproduction of the Cape Sable seaside sparrow, which builds its nest close to the ground. With slow and predictable changes in water level, these birds could start their nesting process according to water-level cues and not have the nests flooded later. Alligator and crocodile nests are similarly vulnerable to water-level fluctuations. If water levels rise too rapidly, the nests can be flooded. If water level falls too fast, the nest may be deserted (Mazzotti and Brandt 1994).

The changes in the Everglades deriving from the water-control structures are large in scale and require landscape-level restoration. The Everglades face other challenges that human activity has imposed in the last several decades, such as storm-water runoff from the phosphorus-enriched Everglades Agricultural Area, mercury pollution, and invading species, but this report focuses on hydrology. In 1995, the state of Florida passed the Everglades Forever Act to initiate restoration of the Everglades and Florida Bay (Hinrichson 1995). Part of the act, the Everglades Construction Project, requires the creation of storm-water treatment areas to remove phosphorus from the water, allowing more water to be directed south. Another project has the aim of improving the delivery of water into Everglades National Park. Currently, this is done through four outlets. By widening these to a 30-km area, the amount of sheet flow can be increased. Other changes are also under way or in the planning stage. The Army Corps of Engineers has been assigned the task of devising an overall plan that will both improve the protection for Everglades National Park and Loxahatchee National Wildlife Refuge and provide sufficient water for a robust urban and agricultural economy. Many other governmental agencies are cooperating in assessing the impact of proposed alternative plans.

This leads to the fundamental question of how to plan the most effective restoration before investing in the costly implementation of reengineering the water regulation system. We present next a modeling approach that attempts to predict the consequences of various landscape hydropatterns to a suite of top consumers in the Everglades.

A MODELING APPROACH

Among the goals of the South Florida Ecosystem Restoration are "maintaining ecological processes (i.e., disturbance regimes, hydrologic processes, nutrient cycles, etc.)" and "maintaining viable populations of all native species *in situ*" (Science Sub-Group 1994). However, predicting whether a chosen restoration plan will accomplish the many specific facets of these general goals requires modeling. A program of the US Geological Survey (USGS) called Across Trophic Level System Simulation (ATLSS) is developing a landscape model for South Florida to supply a set of predictive models. It is beyond the scope of this report to describe all aspects of this modeling effort. The purpose here is to describe the ATLSS approach to modeling some of the faunal components of the Everglades.

The amount of work involved and the paucity of data on many species make it infeasible to model the populations of all native faunal species. However, it is quite possible to model in detail some of the species that are of most concern, either because they are endangered or because they play an important role in the ecosystem. Sufficient data are available on some of these species to develop models with enough mechanistic detail to predict population response to changes in the environment, particularly changes in hydrology that may be implemented as part of the restoration. We suggest that modeling a sufficiently diverse set of such species, particularly top trophic level species, may indicate the prospects for many other species and of ecosystem health as a whole.

The species we have chosen as indicator species are the Florida panther, white-tailed deer, Cape Sable seaside sparrow, snail kite, white ibis, wood stork, great egret, great blue heron, American alligator, and American crocodile. Each of these species is different in its use of the landscape and resources (Davis and Ogden 1994). The Cape Sable seaside sparrow is a habitat specialist with a very limited range. The crocodile is at the northern extreme of its range in Florida. Florida panther, snail kite, and wading bird individuals integrate over large areas of landscape. The alligator is a key species in the system, being both strongly affected by hydrology and exerting a positive effect on many other species through its maintenance of alligator ponds. In all, these species span a range of habitat needs and trophic interactions. Although these species are not surrogates for the whole system, the simultaneous success of all of these umbrella species in a restored Everglades would imply that the system is healthy in many respects.

These umbrella species are modeled in a dynamic, spatially explicit environment provided by Geographic Information System (GIS) information coupled to models of hydrology and other abiotic factors, as well as to aggregated models of the functional groups of prey that these species depend on. The population models themselves are individual-based models. These are models for either single populations or assemblages of interacting populations in which each organism in a population is modeled individually [for example, see Huston and others (1988) and DeAngelis and Gross (1992)]. The characteristics of each organism (age, size, spatial location, sex, health, social status, experience, knowledge, and so on) constitute the variables of the system. Thus, if there are N individuals being modeled at a given time, each with M characteristics, then the model is following the states of $N \times M$ variables. These models contrast with the classic models of population dynamics, such as the logistic equation or Lotka–Volterra equations. In these classic models, individuals are aggregated into population-level variables.

The main reason for choosing a spatially explicit, individual-based approach is that the success of these species ultimately depends on the details of time and energy budgets of individuals in relation to the changing spatial distributions of their prey. Aggregated-variable models often lack the resolution to determine whether the individuals in the population can acquire enough food each day to survive and reproduce. Such models cannot be expected to capture the effects of highly localized changes in a complex, heterogeneous landscape, which may in fact have great consequences for the population as a whole. We next describe the modeling of the dynamic structure of the landscape and two of the individual-based population models.

THE DYNAMIC LANDSCAPE BASE

Figure 2 shows the general structure of the ATLSS modeling approach. There are four levels of modeling in this approach. The individual-based models for indicator species use information from the models at the lower layers. Immediately below the individual-based models are the intermediate trophic levels (fish, aquatic macroinvertebrates such as crayfish and apple snails, and several reptile and amphibian functional groups). These are modeled as size-structured populations and coupled to such top trophic level species as wading birds, alligators,

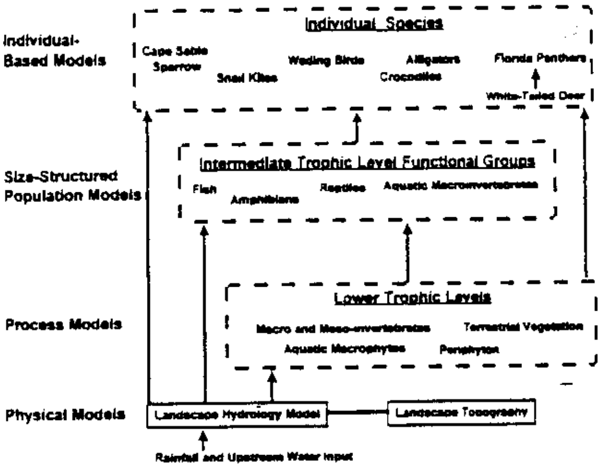


Figure 2. Schematic of the Across Trophic Level System Simulation approach for modeling ecosystems of South Florida. This shows the four levels of modeling used and the direction of effects from abiotic forces and lower and intermediate trophic levels to the higher trophic level species. Feedback effects of higher trophic levels on lower and intermediate levels also occur in the models.

and snail kites. Below this layer, and driving the biomasses of the intermediate trophic levels, are the lower trophic levels, consisting of periphyton, aggregated aquatic mesofauna (for example, nematodes, *Daphnia*) and macroinvertebrates (insect larvae), and macrophytes. The macrophytes include a variety of plant types, including aquatic and terrestrial types that provide forage for white-tailed deer. These lower trophic levels are simulated by process models.

Forming the base for this hierarchy of biotic models is a "landscape structure" in which all static and dynamic information is stored. This includes such standard static GIS information as surface elevations, vegetation types, soil types, and road locations, as well as dynamic information, such as changing water levels across the landscape. The individual-based models for indicator species are designed to make specific predictions. These predictions can be accurate and useful only if the model landscape on which they are simulated is accurately represented. It is crucial, in particular, that the water depths at locations across the landscape be accurate, because foraging and reproductive success of animals are highly dependent on the details of seasonal water-level rise and fall.

Some of the basic features of the layers below the individual-based models are briefly described next.

Description of Vegetation Types

Currently, the model uses a vegetation map prepared for the Florida Gap Analysis Project, with a spatial resolution of 28 × 28-m spatial cells, which we have aggregated to 100 × 100-m cells. The map seems adequate for most purposes and will be continually updated as it is improved. In some cases, the map is too coarse to discriminate vegetative classes important to the indicator species (for example, *Muhlenbergia* grass for the Cape Sable sparrow), so the map is supplemented with on-site information.

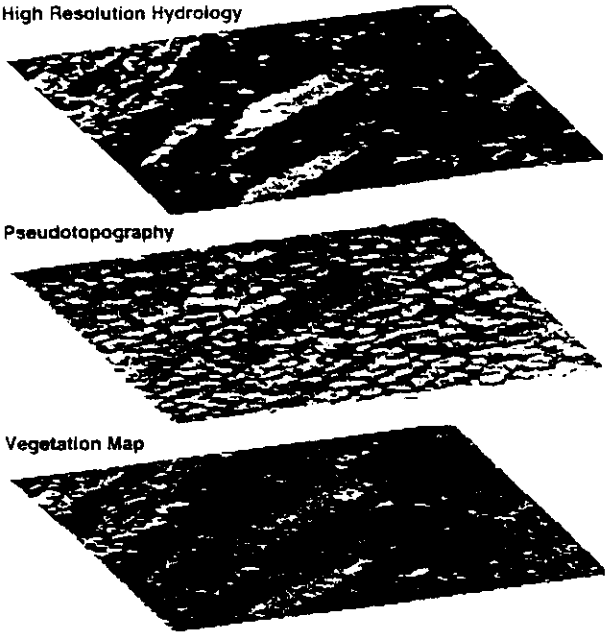


Figure 3. Map layers for a 2 × 4-mile area showing vegetation and pseudotopography derived from the vegetation on 100 × 100-m resolution. The top layer shows the hydrology calculated on a 100 × 100-m scale.

Description of Hydrology

The landscape model is designed to use water depth output from hydrologic models, such as the South Florida Water Management District's Water Management Model (SFWMM) and Everglades Landscape Model (ELM). The spatial resolution at which hydrology is modeled is limited by information on topography. The SFWMM uses 2 × 2-mile cells and the ELM uses 1 × 1-km cells), but this resolution is too coarse to model ecological responses accurately. Because of this, the ATLSS program developed a method to approximate the land surface elevations from current vegetation patterns down to a 100 × 100-m scale; that is, "pseudotopography" (see Figure 3).

Description of Topography

The pseudotopography method combines the known vegetation type in a 28 × 28-m (or aggregated 100 × 100-m) spatial cell with known empirical information on the relationship between mean hydroperiod and the type of vegetation that can result. From this information, one knows the approximate hydroperiod needed to produce a particular vegetation type, and from the output of a hydrologic model, one can estimate the elevation needed to produce the hydroperiod. Using additional constraints imposed by the conservation of water volume, one can then infer spatial elevations at the scale of the vegetation map. From this improved estimate of fine-scale topography, one can predict dynamically changing water levels at this finer scale. Direct topographic data will replace pseudotopography as direct measurements of topography become available at the scales of resolution needed by biological models, but the pseudotopogaphy appears adequate at this point.

Seasonal Vegetative Biomass Dynamics

The seasonal vegetation dynamics model is designed to produce high spatial and temporal resolution across the entire South Florida region for selected vegetation properties of importance to the higher trophic levels in both aquatic and terrestrial food chains. Types of plant tissue are classified on the basis of their forage quality. The definition of forage quality used in the model is based on the energy content (cal/g dry weight) that is available to a ruminant herbivore, specifically white-tailed deer.

Fish and Aquatic Macroinvertebrate Dynamics

The model predicts the fish and important aquatic macroinvertebrate (for example, crayfish) population responses to the seasonal pattern of water levels in all of the spatial cells across the landscape, in order to predict prey availability for wading birds. For example, forage fish for the wading birds are modeled as an age- and size-structured functional group. This use of a structured model is important, both because the wading birds have size-class preferences and because the buildup of fish populations in cells undergoing drying and flooding cycles depends on the age- and size-specific physiological growth and reproduction in the population. The temporal resolution of the model is a 5-day time step, which is short enough to capture fine-scale fish dynamics within a season. The spatial resolution is a 500 × 500-m cell, which is small compared with the spatial gradient, so there is a well-defined average elevation of the cell, yet it is large enough that fish movement across cell boundaries is a first-order effect (compared with zero-order effects of the population within the cell). The fish model results suggest that hydroperiod determines available biomass in a straightforward manner (DeAngelis and others forthcoming). The model simulations are in general comparable with data from the field in the Everglades (Loftus and Eklund 1994).

SPECIFIC INDIVIDUAL-BASED MODELS

Only two of the individual-based models developed for ATLSS are discussed here: the model for colonial wading birds (specifically wood storks here) and the model for the interaction of the white-tailed deer and Florida panther.

Wading Bird Assemblage: Wood Storks

The causes for the declines in wading birds mentioned earlier have been the object of empirical study for over a decade. Aerial surveys (systematic reconnaissance flights) have been performed over a number of years to explore the environmental factors influencing the nesting sites and nesting success (Bancroft and others 1994; Hoffman and others 1994). In these surveys, biweekly estimates were made of nest sites and foraging densities of several wading bird species (great egrets, white ibises, wood storks, and great blue herons) on 2 × 2-km cells across the landscape, along with categorization of vegetation types and water-level conditions (wet, transitional, or dry) of the cells.

Wading birds nest in colonies close to sites of prey availability (generally not much more than 9 km maximum, except for wood storks, which can soar long distances) (Bancroft and others 1994). Many observers of the Everglades believe that the changes in water regime during the past several decades, plus the drainage of short-hydroperiod wetlands to the east of the current Everglades, have affected reproductive success of wading birds [for example, see Kushlan (1986), Fleming and others (1994), Bancroft and others (1994), Ogden (1994), and Hoffman and others (1994)]. These short-hydroperiod wetlands dry out early and provide wading birds enough available prey to make an early start on nesting. Water regulation has resulted in ponding of overland flows in northern reaches of the Everglades catchment area (WCAs) and severe overdrainage of the southern reaches downstream of these impoundments. Collectively, these changes have altered the locations and spatial arrangement of seasonal foraging habitats for wading birds, in addition to reducing their areal extent.

The focus of present modeling efforts (Fleming and others 1994; Wolff 1994) for wading birds is to develop simulation models that enable the prediction of the dynamics of colonies and the nesting success of wading birds in relation to different hydrologic scenarios and the resulting spatial and temporal distribution of their prey. The species selected for modeling use tactile cues (wood stork and white ibis) and visual cues (great egret and great blue heron) in their feeding and represent the majority of the wading bird population in the Everglades and Big Cypress ecosystem of southern Florida.

Because wading birds depend on patchy resources and can travel long distances during their foraging flights, models aggregated to the population level are inappropriate to describe the dynamics of colonies in a heterogeneous and rapidly changing environment such as the Everglades/Big Cypress ecosystem. Although most activities of wading birds occur on small time scales (minutes or hours), these detailed activities nevertheless have a large influence on the overall foraging success of individual birds, as well as the depletion of local prey resources. Individual-based modeling, in which individual birds are described by a set of rules that govern their activities, seems to be an appropriate way to describe this situation.

The model consists of species-specific sets of rules for the behavior and the energetics of nesting adults, as well as rules for the energetics and growth of their nestlings. The model uses the output of the landscape, hydrology, and fish and aquatic macroinvertebrate models within ATLSS. These data are then used by the individual birds, for example, to determine at which sites they can forage and how successful they are at these sites.

An early version of the current wading bird model was developed by Wolff (1994), in which a single colony of wood storks (*Mycteria americana*) was simulated at a traditional colony site and simulated different scenarios in which he decreased the areal extent of peripheral wetlands that represent early shallow-water foraging habitat for wading birds. Colonies were formed if the birds found sufficient food in high-density patches, which both triggered a nesting response and provided female birds with the additional energy required for egg production. In the simulation, the larger the reduction in peripheral wetlands area, the later was colony formation (Figure 4a). In addition, the number of nesting attempts decreased for larger delays in colony formation (Figure 4b). Both of these patterns can be attributed to a shortage of high-density food patches during the early dry season. There was enough food available for the birds to meet their basic energy requirements, but not enough to trigger nesting or egg production. The number of fledglings decreased sharply in the model with the reduction in peripheral wetlands area and was always well below the possible production that would have occurred if every nesting attempt had produced three fledglings (Figure 4c). If the parents could not provide their chicks with sufficient food, broods were reduced. If the adult birds failed to meet their own energy requirements, they deserted the colony. These general patterns of delay in colony formation, reduction in the number of nesting attempts, and lower numbers of fledglings, were quite robust for all scenarios in which the areal extent of peripheral wetlands was decreased.

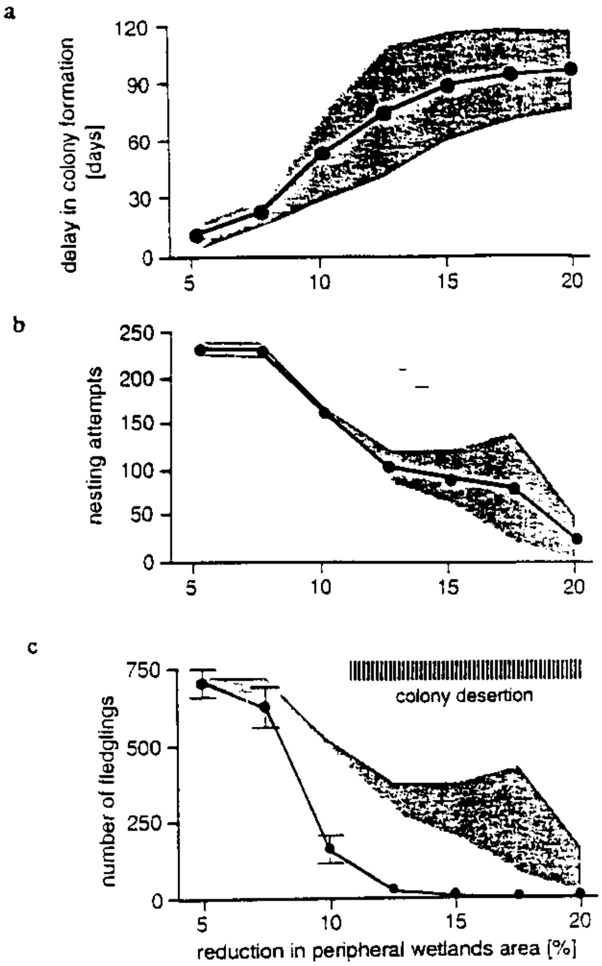


Figure 4. Output from the wading bird model specialized to wood storks [based on Wolff (1994)]. Delay in wood stork colony formation (a), number of nesting attempts (b), and number of successful fledglings (c), when the total area of the peripheral wetlands was reduced by 5% up to 20% relative to the natural landscape. The simulations were run for a colony of 250 pairs. The shaded area indicates the variation of 500 simulation runs.

An expanded version of the model simulates wading birds in several, mixed-species colonies and has been largely completed for the freshwater areas of the Everglades/Big Cypress ecosystem. The rules describing the behavioral activities and the energetics of individual wading birds other than wood storks are parameterized as far as existing data permit. The mangrove areas are assumed to be critically important during the early part of the breeding season, so the wading bird model must be extended to these areas as well. An extension to these areas will be possible as soon as the corresponding models for the hydrology and the prey resources are available for these areas.

Florida Panther and White-tailed Deer Trophic Interaction Modeling

The Florida panther (*Felis concolor coryii*) represents one of the most challenging problems in conservation. This population is the remnant of a population that once was found throughout the Gulf and Atlantic coastal plains of the southeastern United States (Young and Goldman 1946). The total population of panthers in southern Florida probably includes no more than 50 adults, and this subspecies was listed as endangered in 1973. Smith and Bass (1994) point out that the Everglades/Big Cypress system is not high-quality panther habitat compared with upland areas farther north, but its relative freedom from human impact makes it currently "the only realistic theater for a wild panther population." They thus ask, "Is this area adequate to sustain a population of panthers in the long run?"

Studies of radio-collared panthers have shown that their movements and use of habitat within the Everglades are nonrandom. Breeding females, in particular, tend to locate in areas of high deer densities where there is sufficient cover for hunting (Smith and Bass 1994). The edge between upland forest and open prairie is particularly favorable habitat. Much of this edge lies outside of areas that are directly affected by water management. However, models can be used to help determine the carrying capacities of various landscapes within southern Florida for the panther and assess the usefulness of protection of land not currently protected that may increase the overall carrying capacity.

Therefore, as part of ATLSS, a model has been developed that will enable the determination of the potential long-term impacts (for example, over 30 years or more) of spatially explicit modifications in habitat (particularly hydrology) on the panther population (Comiskey and others 1997). The spatio-temporal dynamics of habitat coupled with small population size and long-distance movements of panthers imply that an individual-based modeling approach offers the best hope to utilize the extensive available empirical data on panthers to produce a model that appropriately tracks the effects of alternative hydrologic scenarios. Additionally, such a model would provide cost-effective methods to help guide potential captive-release programs. The models could be tested by comparing the effect of alternative release programs on the model population.

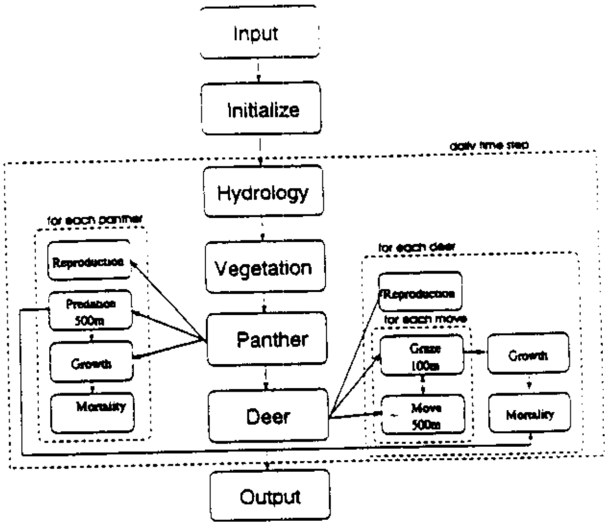
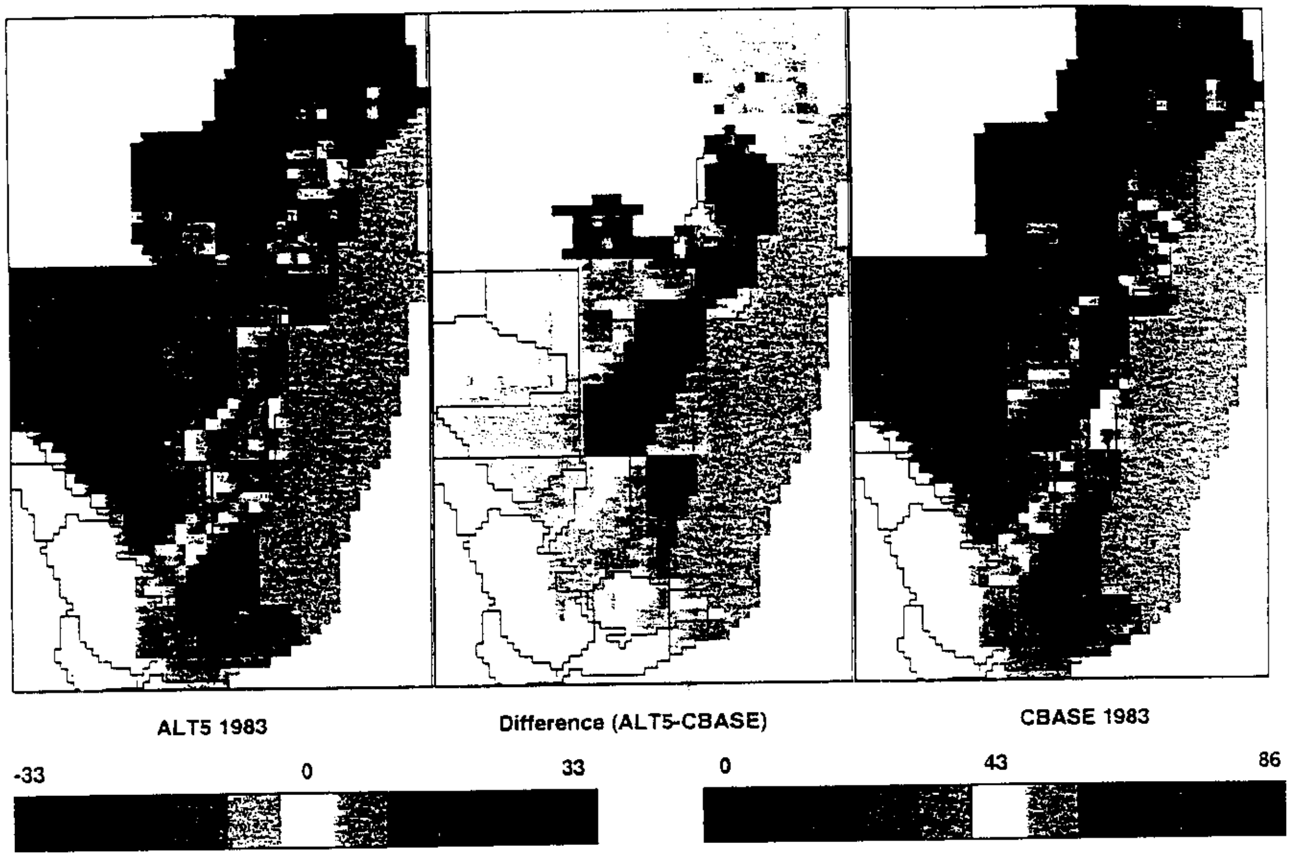


Figure 5. Schematic of Florida panther–white-tailed deer model (Comiskey and others 1997).

Individual panther success (that is, survival and reproduction) in South Florida is closely linked to a panther's ability to obtain large prey items, notably white-tailed deer (*Odocoileus virginianus seminolus*) and feral hogs. Thus, to produce a panther model, it was essential to develop an individual-based model of white-tailed deer to determine how hydrologic changes would affect these key prey resources and to link this to the panther model. White-tailed deer, the only large (native) herbivore in the region, have a significant localized impact on vegetation, so including them as a major component of the project is justified independent of the importance of deer to panthers. Accounting for the impacts on vegetation of feral hogs in the system would also be appropriate. At present, however, the model does not include feedback from local hog densities on vegetation. A schematic of the coupled Florida panther–white-tailed deer model is shown in Figure 5.

The main objective of this modeling component is to predict the relative impacts of alternative hydrologic scenarios over a 30-year time frame on the spatial and temporal (for example, seasonal) distribution of panther and deer across South Florida,



Mean Ponding1983

Figure 6. An index of ponding, or average water depth, across the South Florida landscape, calculated from the South Florida Water Management Model using the rainfall pattern for the year 1983 and using both the current water regulation structures (CBASE, **left panel**) and the Alternative 5 structures (AT5, **right panel**). The middle **panel** shows differences between these scenarios. The *left color bar* (on the left side below the maps) refers to the central (difference map) and has 11 colors. The color in the middle of the bar (corresponding to the value zero) is *white*. Negative differences are indicated toward the left, with increasing negative values having deeper shades of *red*. Positive differences (that is, ALT5 greater than CBASE) are indicated by *grays* increasing in darkness toward the right, to *black* for the greatest differences. The *second color bar* shows *red* corresponding to the lowest values in the CBASE and ALT5 maps, increasing through *yellow* to *green* and finally *blue* for the highest values.

and to produce relative comparisons of mortality, reproduction, individual movement patterns, and territory size across the landscape for both species.

The model operates on a daily time step although, within this time step, deer and panther movements are simulated, taking account of local water conditions, forage, and prey availability. Spatially, the model uses vegetation data to calculate forage availability on a 100-m scale, but tracks deer and panther locations on the daily time step at 500-m scale.

The primary inputs to the Florida panther–white-tailed deer model are daily hydrology data at the 100-m scale (available through a pseudotopography model; see above), a vegetation map (from which dynamic forage maps with three quality levels of forage are constructed), a land-use map, a map of feral hog density, and a road map. The primary environmental factors driving the model are, therefore, hydrology and vegetation, which vary temporally and spatially.

The white-tailed deer–Florida panther and other models are used to make comparisons between different hydrologic scenarios proposed for restoration of southern Florida ecosystems. Various types of comparisons are being performed, including total population means, variances, and spatial distributions through time. In addition, one can also compare the habitat suitability for components of the life cycle of species. For example, how would modified water management in the Everglades/Big Cy-

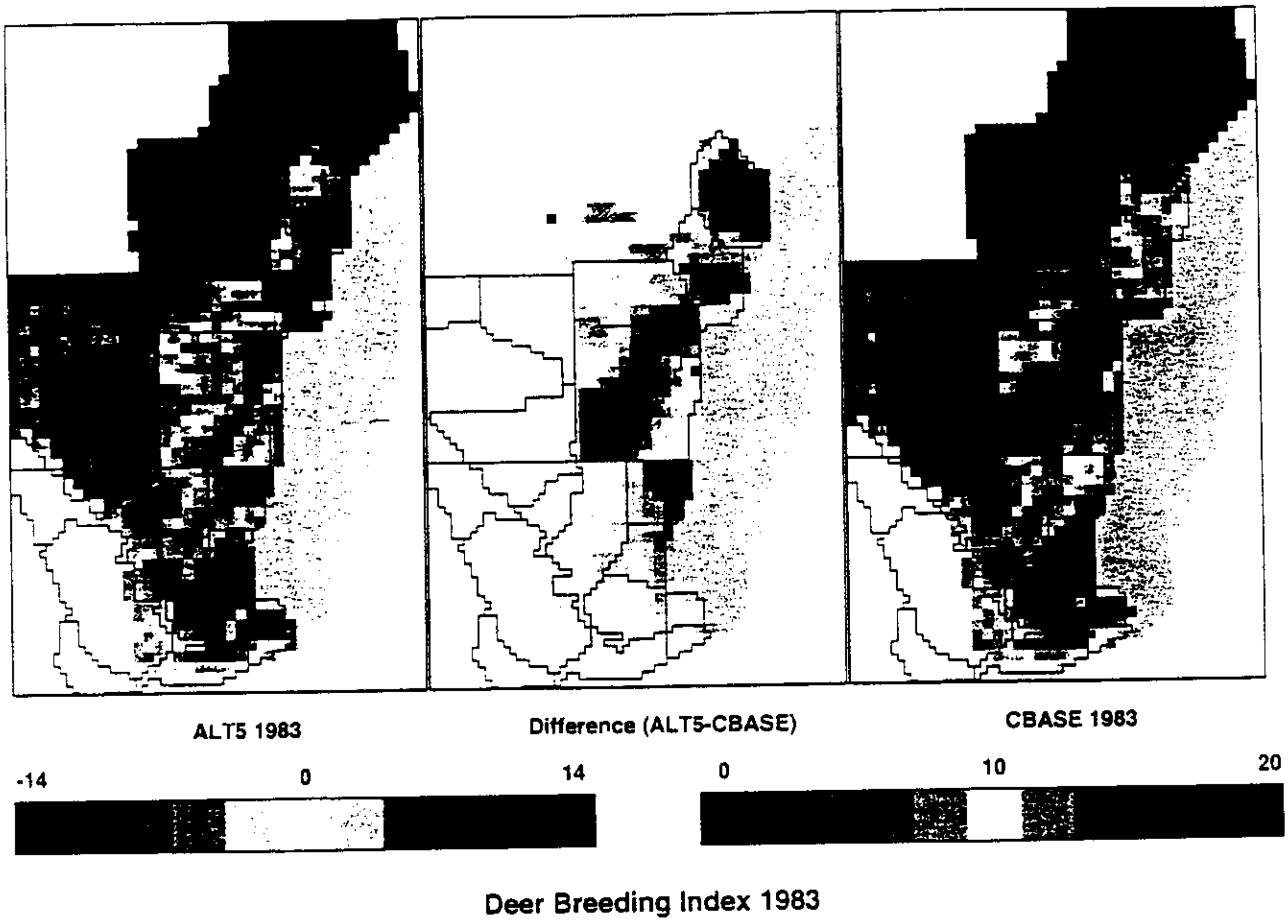


Figure 7. An index of white-tailed deer reproduction (Deer BI) is calculated from the model using the rainfall pattern for the year 1983. The left panel shows the predictions for the current water regulatory structures (CBASE), the right panel shows the predictions under Alternative 5 structures (ALT5), and the middle panel shows the differences between these scenarios. The *color coding* in this figure is the same as in Figure 6.

press region affect the usefulness of habitat for white-tailed deer reproduction. Some preliminary simulations have been performed to compare a modified water-delivery plan (Alternative 5 or ALT5) with the existing water-delivery plan (CBASE). Figure 6 shows an index of ponding, or water depth, averaged over the year, using 1983 rainfall data in the SFWMM (see the figure caption for color coding). Under ALT5 (the left panel), ponding is slightly greater in the southern areas of the figure (Everglades National Park), much greater in some far-northeastern areas (WCAs 1 and 2), and less in the central areas just north of Everglades National Park (WCA 3A) when compared with CBASE (the right panel). The differences between the two scenarios are shown in the middle panel. Ponding has a negative effect on fawning. This magnitude of this effect is calculated by the deer reproductive algorithm in the model. Figure 7 shows the consequent pattern of differences in the reproductive potential of deer (Deer BI) as a function of spatial location. Relative to CBASE, the ALT5 scenario leads to a slight decrease in Deer BI in WCAs 1 and 2, and a substantial increase in Deer BI in WCA 3.

The deer reproductive potential shown in Figure 7 is only part of the overall model. The full model produces highly detailed survival and spatial distribution information on deer and panther distribution pattern changes over time. Figure 8 shows model predictions of the distribution of nearly 10,000 deer at eight different instants of time. Validation efforts include detailed comparisons of deer distributions with historical data, comparison of aggregated variables such as age-dependent mortality, age structure, body weight distribution, and birth rates with available data, and comparison of modeled individual-movement patterns with radio-collar data.

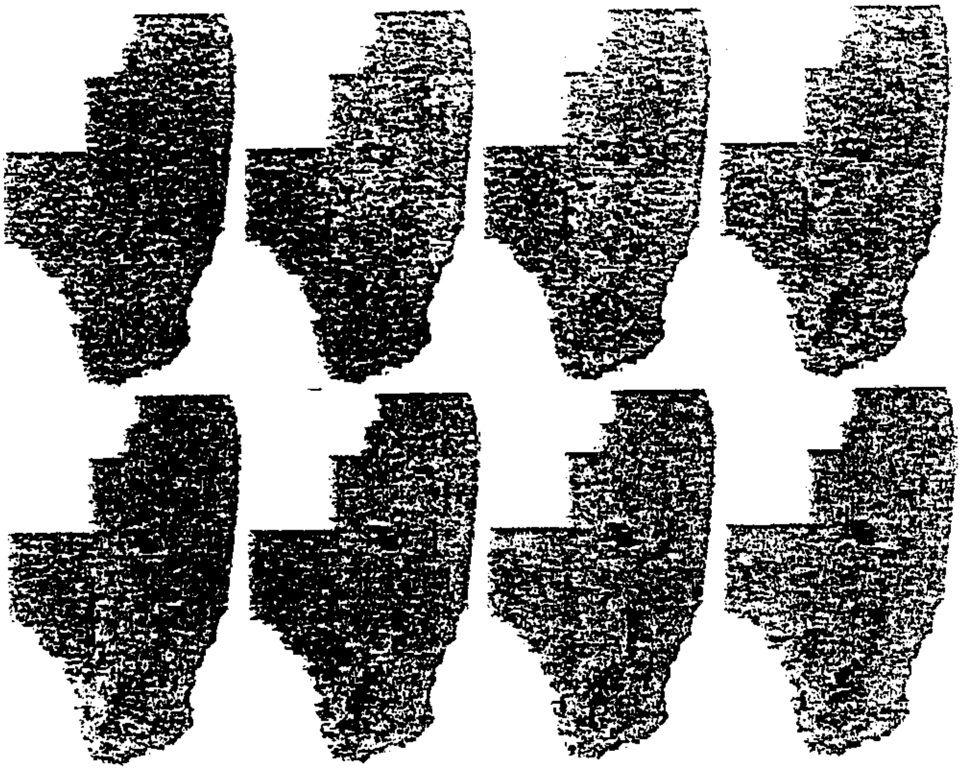


Figure 8. Model predictions of spatial patterns of white-tailed deer at eight different times, reflecting the response of deer to water depth and vegetation forage availability.

DISCUSSION

This report describes use of spatially explicit landscape modeling, together with individual-based modeling of a set of higher trophic level indicator species, to provide quantitative predictions relevant to the planned Everglades restoration. The work is still in progress and none of the models discussed have been fully tested against historical data. At present, predictions made by these models must be used with caution and only after interpretation by experts on the various aspects of South Florida ecosystems. However, we expect them to be useful in providing information to help to rank the effectiveness of various water management options against specific criteria for the indicator species, such as reproductive success. The models should be capable of indicating how sensitive various species are to different hydrologic conditions. As the models are tested against continuing monitoring studies of the species and other ecological components, their parameters will be refined and their predictive capacities should improve.

The ATLSS program may be the largest application yet attempted of individual-based modeling to an environmental issue. Whether or not this approach works in application to the Everglades will have implications for other applied problems.

In our view, spatially explicit, individual-based modeling finds itself at the crossroads of two important theoretical issues and many major environmental issues. The theoretical issues involve uniting or at least connecting in a strong way (a) population ecology with the physiological and behavioral ecology of individuals and (b) population ecology with ecosystem ecology. The models discussed here certainly address the first issue. The populations are modeled purely on the basis of individual-level behavioral and physiological rules. The second issue is also addressed as well. The ecosystem influences on the population are incorporated directly through effects on individuals. The rules governing the individuals include their responses to all of the relevant habitat factors and resource availabilities. The individual is the natural linkage between the population and ecosystem (Huston and others 1988).

The environmental issues are multitudinous, as species extinctions and ecosystem destruction continue at a rapid pace around the world. Restoration and conservation ecology require the development of ways to analyze and mitigate the effects of humans on natural populations. We agree with others [for example, Pulliam and Dunning (1995) and Turner and others (1995)] that, to assist in these objectives, it is essential to develop models with a great deal of detail in the description of the landscape and the way that plants and animals respond to the landscape.

ACKNOWLEDGMENTS

This work was funded by the US Geological Survey, the National Park Service, and the US Army Corps of Engineers through cooperative agreements between the US Geological Survey and the University of Tennessee and the University of Miami.

REFERENCES

Bancroft GT, Strong AM, Sawicki RJ, Hoffman W, Jewell SD. 1994. Relationships among wading bird foraging patterns, colony locations, and hydrology in the Everglades. In: Davis SM, Ogden JC, editors. Everglades: the ecosystem and its restoration. Delray Beach (FL): St Lucie. p 615–58.

Browder JA, Gleason PJ, Swift DR. 1994. Periphyton in the Everglades: spatial variation, environmental correlates, and ecological implications. In: Davis SM, Ogden JC, editors. Everglades: the ecosystem and its restoration. Delray Beach (FL): St Lucie. p 379–418.

Comiskey EJ, Gross LJ, Fleming DM, Huston MA, Bass OL, Luh H-K, Wu Y. 1997. A spatially-explicit individual-based simulation model for Florida panther and white-tailed deer in the Everglades and Big Cypress landscapes. Proceedings of the Florida Panther Conference, Fort Myers, FL, Nov 1–3, 1994. Dennis Jordan (ed.), U.S. Fish and Wildlife Service, p 494–503.

Davis SM, Ogden JC, editors. 1994. Everglades: the ecosystem and its restoration. Delray Beach (FL): St Lucie.

DeAngelis DL, Gross LJ, editors. 1992. Individual-based models and approaches in ecology. New York: Chapman and Hall.

DeAngelis DL, Loftus WF, Trexler JC, Ulanowicz RE. Modeling fish dynamics and effects of stress in a hydrologically pulsed ecosystem. J Aquat Ecosyst Stress Recov. Forthcoming.

Duever MJ, Carlson JE, Meeder JF, Duever LC, Gunderson LH, Riopelle LA, Alexander TR, Myers RL, Spangler DP. 1986. The Big Cypress National Preserve. Research Report nr 8. New York: National Audubon Society. 455 p.

Fennema RJ, Neidrauer CJ, Johnson RA, MacVicar TK, Perkins WA. 1994. A computer model to simulate natural Everglades hydrology. In: Davis SM, Ogden JC, editors. Everglades: the ecosystem and its restoration. Delray Beach (FL): St Lucie. p 249–90.

Fleming DM, Wolff WF, DeAngelis DL. 1994. Importance of landscape heterogeneity to wood storks in Florida Everglades. Environ Manage 18:743–57.

Hinrichson D. 1995. Waterworld. Amicus J 17:23–7.

Hoffman W, Bancroft GT, Sawicki RJ. 1994. Foraging habitat of wading birds in the Water Conservation Areas of the Everglades. In: Davis SM, Ogden JC, editors. Everglades: the ecosystem and its restoration. Delray Beach (FL): St Lucie. p 585–614.

Huston MA, DeAngelis DL, Post WM. 1988. New computer models unify ecological theory. BioScience 38:682–91.

Kushlan JA. 1986. Responses of wading birds to seasonally fluctuating water levels: strategies and their limits. Colonial Wading Birds 9:155–62.

Light SS, Dineen JW. 1994. Water control in the Everglades: a historical perspective. In: Davis SM, Ogden JC, editors. Everglades: the ecosystem and its restoration. Delray Beach (FL): St Lucie. p 29–46.

Lodge TE. 1994. The Everglades handbook. Delray Beach (FL): St Lucie. 228 p.

Loftus WJ, Eklund A-M. 1994. Long-term dynamics of an Everglades small-fish assemblage. In: Davis SM, Ogden JC, editors. Everglades: the ecosystem and its restoration. Delray Beach (FL): St Lucie. p 461–84.

Mazzotti FJ, Brandt LA. 1994. Ecology of the American alligator in a seasonally fluctuating environment. In: Davis SM, Ogden JC, editors. Everglades: the ecosystem and its restoration. Delray Beach (FL): St Lucie. p 485–505.

Ogden JC. 1994. A comparison of wading bird nesting colony dynamics (1931–1946 and 1974–1989) as an indication of ecosystem conditions in the southern Everglades. In: Davis SM, Ogden JC, editors. Everglades: the ecosystem and its restoration. Delray Beach (FL): St Lucie. p 553–70.

Pulliam HR, Dunning JB Jr. 1995. Spatially explicit population models: current forms and future uses. Ecol Appl 5:3–11.

Science Sub-Group. 1994 Sep. South Florida ecosystem restoration: scientific information needs. Draft. Management and Coordination Working Group, Interagency Task Force on the South Florida Ecosystem.

Smith TR, Bass OL Jr. 1994. Landscape, white-tailed deer, and the distribution of Florida panthers in the Everglades. In: Davis SM, Ogden JC, editors. Everglades: the ecosystem and its restoration. Delray Beach (FL): St Lucie. p 693–708.

[SFWMD] South Florida Water Management District. 1992. Surface water improvement and management plan for the Everglades: supporting information document. West Palm Beach (FL): SFWMD. 472 p.

Turner MG, Arthaud GJ, Engstrom RT, Hejl SJ, Liu J, Loeb S, McKelvey K. 1995. Usefulness of spatially-explicit population models in land management. Ecol Appl 5:12–6.

Wolff WF. 1994. An individual-oriented model of a wading bird nesting colony. Ecol Modell 72:75–114.

Young SP, EA Goldman. 1946. The puma: mysterious American cat. New York: Dover. 358 p.