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"A Spatially-explicit Individual-based Simulation Model for Florida Panther and White-tailed Deer in the Everglades and Big Cypress Landcapes"

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These are preliminary lecture notes, intended only for distribution to participants.

A Spatially-explicit Individual-based Simulation Model for Florida Panther and White-tailed Deer in the Everglades and Big Cypress Landscapes[1]

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1 Introduction

The White-tailed Deer/Florida Panther Model presented herein is one component of the ATLSS family of models (Across Trophic Levels System Simulation for the Everglades and Big Cypress Swamp) [2]. ATLSS activities are coordinated by the National Biological Survey (NBS). The goal of ATLSS is to provide a total ecosystem approach to the complex environmental situation in South Florida. One of the objectives of ATLSS is to provide a framework for analyzing the effects of alternative water management scenarios in South Florida on the long-term population dynamics of key biotic components of the system. This objective is being accomplished by producing a series of models at various trophic levels, with the capability to integrate these models across levels. Models for components of the lower trophic levels (e.g., periphyton, aquatic macrophytes, detritus, zooplankton, and benthic insects) will be ecosystem process models. Age- and size-structured models will be used for the intermediate trophic levels (e.g., macroinvertebrates and fish). Models for the large consumers of the system will be individual-based. In addition to white-tailed deer and Florida panther, individual-based spatially-explicit models are being constructed for the American alligator and for several wading bird species. Integration of ATLSS model components is coordinated by the Institute for Environmental Modeling at the University of Tennessee, with support from Everglades National Park (ENP) and NBS.

A spatially-explicit model is grid-based, with the landscape divided up into spatial cells. Within this spatial grid, individual-based models track the states of each individual within a population. Each individual has a state consisting of its location, sex,

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age, body weight, etc. Decision rules, which are a function of the states of each individual, determine how individual animals move across the landscape, interact with one another and respond to their environment. The Deer-Panther Model also contains stochastic components in behavior decision-making. For example, when a fawn is born, there is a 50/50 probability that it will be male (or female). The probability that twins will be born increases with the health status of the mother.

Two adult female deer have the same decision tree of behavior rules in the model, but because of differences in individual characteristics, such as health, reproductive status or location on the landscape, they may behave differently. The health status of an individual reflects its history of weight gain and loss during the simulation. Two individuals located on different parts of the landscape, and thus confronted with different local conditions for environmental variables such as water depth and available biomass, will in general behave differently even if all other state components of the individuals are the same. Individuals mate at different times, consume differing amounts of forage, and gain or lose weight depending on local forage availability, individual bioenergetic status, and stochastic factors.

2 Study Area

The landscape of South Florida is covered by a complex mosaic of vegetation types. The current data on vegetation distribution used in the Deer-Panther Model is the South Florida portion of the Florida Department of Transportation (DOT) vegetation map, which is based on satellite imagery at 30-m resolution. The map includes twenty-two vegetation types and covers about 10,000 mi^2. It will be updated soon with a post-Hurricane Andrew vegetation map developed by the University of Georgia and the National Park Service. The model area for the Deer-Panther Model is currently restricted to the area for which hydrologic data are available, cutting off the portion west of U.S. 29 (which includes Fakahatchee Strand and the Florida Panther National Refuge) but encompassing most of South Florida from Lake Okeechobee in the north to Florida Bay (about 7,500 mi^2). When the western region is added to the hydrology models, this area will be included in the Deer-Panther Model.

Major areas of interest for the model are:

- Big Cypress National Preserve, composed mainly of cypress swamp mixed with pinelands, marsh, and hardwood hammock (700,000 acres).
- Everglades National Park (ENP) to the south, extending into Florida Bay (about 1,500,000 acres). The freshwater systems of ENP, consisting mainly of sawgrass marshes with cypress and bay heads, are currently included in the model area.
- Water Conservation Areas 1, 2, and 3 (almost 900,000 acres). These are large artificial impoundments formed in the early 1960's to prevent flood and drought in agricultural and urban areas to the north and east of the Everglades.

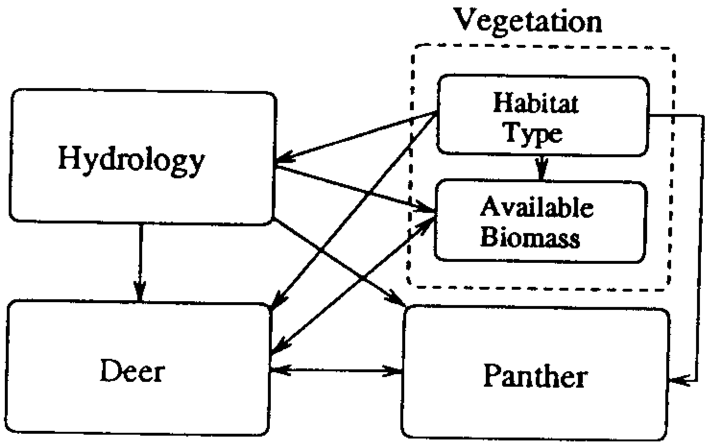

Figure 1: Main Components of Deer-Panther Model

The most prevalent habitat type is freshwater marsh and forested wetlands, occurring throughout the central Everglades and Big Cypress Swamp. The tree islands and hardwood hammocks which are interspersed throughout the wetland areas are important habitat for deer and panthers, providing bedding sites and high ground during the wet season. They provide escape cover from hunters and predators for deer and hunting cover for panthers [6].

The terrain of the study area is almost flat. Elevations range from 10-m in the north to 1-m in the south, sloping gradually at a rate of only a few inches per mile. Mean annual rainfall in the study area is about 55–65 inches, but amounts as high as 120 inches have been recorded in wet years. Eighty percent of the rain falls during the wet season, from May to October, while the dry season has moderate temperatures and little rainfall. Seasonal changes in vegetative components of ecosystem structure and functioning are driven more by rainfall than by temperature or photoperiod [3].

3 Model Components

The Deer-Panther Model has four main components: hydrology, vegetation, deer, and panthers. Figure 1 shows how these components interact. Hydrology inputs drive the model, influencing vegetation growth and restricting movement for deer and panthers. Deer consume available biomass and serve as prey for panthers. Panther predation is a major factor affecting deer mortality.

The Deer-Panther Model is coupled to PV-WAVE, a software application for visual representation and statistical analysis of data. Model outputs can be displayed during execution, or states can be saved at specified times during a simulation for static display and analysis at a later time. The current run-time visualization panel displays four spatial maps showing daily changes in water depth, biomass, and deer and panther distributions over the landscape as the simulation progresses. The user can specify additional outputs for display. In static displays, the user can choose any two regions from the map and display histogram plots for comparison of deer or panther characteristics, such as sex ratios, age or weight distributions, reproductive status or recruitment rates between these two areas.

A model interface is being developed which will allow the user to vary model input parameters and to specify which outputs will be saved from a simulation for later analysis.

3.1 Hydrology

Water level inputs to the model are derived from either of two hydrology models for South Florida, developed by the South Florida Water Management District and Everglades National Park [1].

1. The South Florida Water Management Model (SFWMM) simulates present day hydrology, with all the canals, levees, pumps, and other control structures in place.

2. The Natural Systems Model is a version of the SFWMM with control structures removed. It gives an approximation of the hydrologic patterns of an unmanaged Everglades ecosystem by simulating overland flows.

Both hydrology models take as inputs elevation and historical daily rainfall and evapo-transpiration data from the period 1965 through 1989. Both output daily water depth, but averaged weekly and monthly data have also been computed to provide a choice of inputs to the Deer-Panther Model. When outputs for the two hydrology models are compared, a substantial difference in the quantity and timing of flows is evident, consistent with characteristics of the natural Everglades, which had more wetland areas, longer hydroperiods and deeper ponding levels than the present-day system [1].

The level of spatial resolution for elevation input and for water depth output for both models is 2-mi. x 2-mi. This scale is too coarse to be useful in modeling individual animal movements or predicting vegetation growth at the 100-m scale of resolution. To generate water level heterogeneity at the 100-m level of resolution, water depth outputs from the 2-mi. x 2-mi. cells are redistributed to 100-m x 100-m pixels, based on expected relative depths for the vegetation types represented in each 2-mi. x 2-mi. cell. This results in a 100-m resolution map which approximates the water level at each vegetation pixel.

3.2 Vegetation

The short-term objective of the vegetation submodel is to provide spatial and temporal variation in available forage for the deer herd. Because the model area involved is large, the model employs habitat type maps at two spatial scales of resolution, 500-m and 100-m, which are aggregations of the more detailed 30-m DOT vegetation data. Available biomass values are also computed at these two scales.

Table 1: Three Quality Classes of Vegetation

Class Description	Caloric Content (kcal/kg)	Quantity (kg/ha)
1–High quality forage	1800	2 - 10
2–Medium quality forage	1200	4 - 40
3–Low quality forage	800	unlimited

Three quality classes of biomass are defined for deer foraging based on caloric content (Table 1.) In the model, the amount of biomass in each forage class is updated daily for effects of foraging by deer and at 1, 7, or 30 day intervals (depending on the update option chosen) for effects of seasonal vegetation growth and deterioration. Deer are very selective feeders [4]. They search for plants high in protein and caloric content, and eat all the high calorie forage they can find before they turn to forage of a lower quality.

Class 1 forage will sustain a high demand deer, such as a pregnant or lactating female. Class 2 forage will provide enough energy for an average deer to maintain, but not gain, weight. Class 3 forage is unlimited in quantity from the point of view of the deer, but the caloric content is so low that it can satisfy only about 80% of an average deer's daily energy needs. If only Class 3 forage is available for an extended period of time, deer will lose weight and eventually die.

A more complex vegetation component will be developed over the next two years to provide the model with a greater capability to predict vegetation response to natural disturbances and changes in hydroperiod and nutrient availability. Separate submodels will be incorporated to provide fine-scaled vegetation responses to fire, freeze, and hurricanes.

3.3 White-tailed Deer

The white-tailed deer is the largest herbivore in South Florida. Deer are a major source of prey for the endangered Florida panther and they are also popular game animals.

The deer component of the ATLSS Deer-Panther Model is driven by hydrology and vegetation inputs and is coupled to the Panther Submodel to simulate predator-prey dynamics (see Figure 2). Water level and biomass data are provided for each 500-m x 500-m and 100-m x 100-m spatial cell by the hydrology and vegetation submodels at daily or weekly intervals, depending on the level of detail needed.

At the start of a simulation, each member of the deer population is assigned a state consisting of individual characteristics which are updated daily throughout its lifespan. Some of the autecological characteristics maintained for each individual are location in

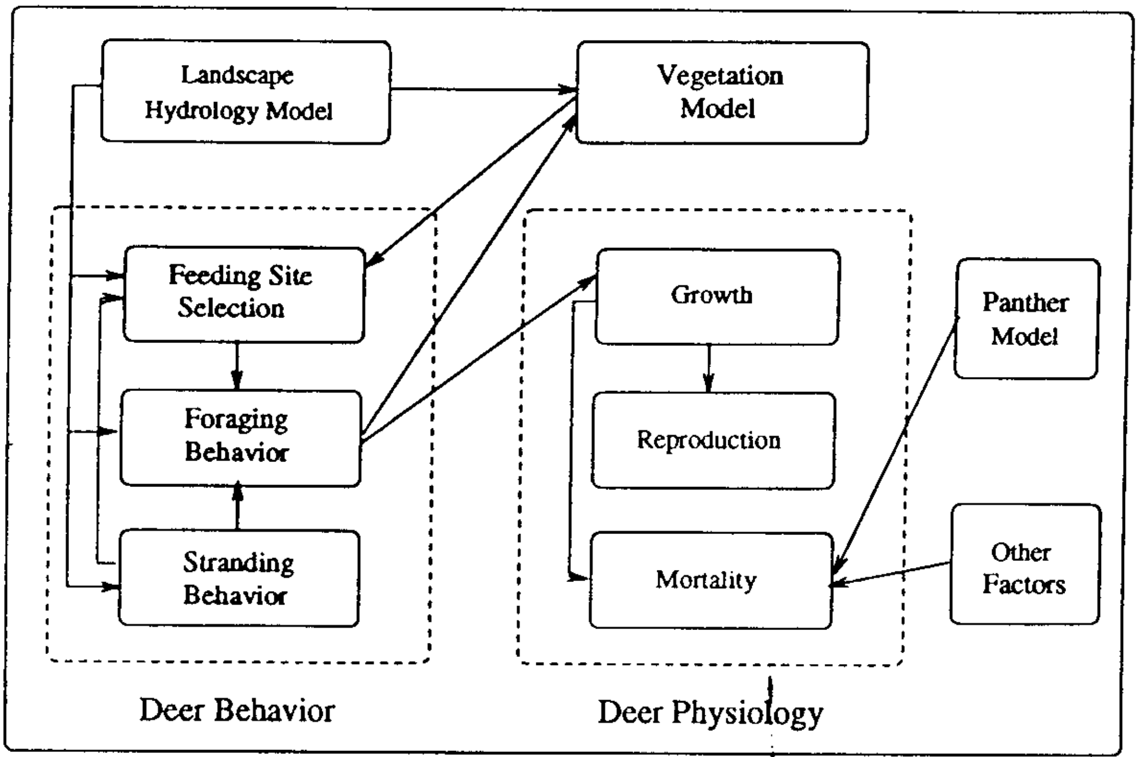

Figure 2: Structure of Deer Component of Deer-Panther Model

the study area, age, sex, weight, maximum weight ever attained, reproductive status, and parent-offspring relationships. For a given simulation, the deer population can be initiated with randomly generated locations and pre-determined sex and age-class ratios or with distributions and individual states saved from a previous simulation.

Deer foraging and growth are modeled on a daily basis. Growth is a function of deer weight, caloric intake, and energy expenditures associated with maintenance, travel, grazing, and reproduction. Weight gain or loss on a given day depends on whether energy intake from foraging is greater or less than energy expenditure for the day. Reproductive success depends on stochastic factors and on the health of the female, as determined by comparing her present weight with her maximum weight ever attained.

Two spatial scales, corresponding to strategic vs. tactical decision-making, are used in the model to simulate deer movement and grazing. Strategic decisions about where to forage on a given day presume some knowledge of the landscape within a deer's activity area. Tactical decisions are low-level decisions related to where within the chosen plot foraging actually takes place. Deer move and select feeding sites at the 500-m level of resolution, choosing the nearest (25 hectare) pixel with high-quality vegetation for foraging. Once a pixel has been chosen, deer forage selectively at the 100-m (1 hectare) level of resolution within that pixel. The maximum distance deer are allowed to move in a day differs for bucks, does, and does with fawns. Deer are limited in their movements and food intake by water depth, with this restriction also differing for bucks, does, and fawns. Stranding, an important source of mortality for deer in some parts of the Everglades during the wet season, is simulated at the 100-m level of resolution.

Male fawns disperse from the mother's location at 18 months of age, while females may stay with the mother in family groups for many years if food is plentiful.

Mortality for deer results from starvation, predation, or other factors. Starvation is identified by comparing each deer's body weight daily to the maximum weight ever attained. Death occurs when a deer's weight drops below 70% of that maximum. Predation by panthers is a significant cause of mortality in the study area and in the model. When deer are its main prey, a panther kills about one deer per week to ten days. At this rate, 40 panthers in the study area could theoretically kill about 2000 deer per year. Bobcats, another important predator of deer in parts of the Everglades and Big Cypress, are not modeled as individuals at this time, but are included in an aggregated "other sources of mortality". Mortality from road hazards, hunting, bobcat predation, injury and disease are treated as stochastic mortality factors in the model. Risks from highway accidents and hunting will be assigned region- or pixel-specific probabilities in the near future when the addition of new map layers for highways, landuse, and regional boundaries enable these risk probabilities to be assessed.

3.4 Florida Panther

The Florida panther, once common throughout the coastal plains of the southeastern United States, is now an endangered species. South Florida contains the last remaining population, estimated at about 30 individuals. Since the few remaining panthers have been so intensively studied, a fairly detailed data base is available for the population. Because the ATLSS Deer-Panther Model is individual-based, the panther component can make use of much of this autecological information, such as the sex, age, weight, health status, and location of each panther. The model offers a choice of options for defining panther population parameters at the start of a simulation. Initial conditions can be based on empirical data for the existing population, or data for a hypothetical population with any pre-defined set of characteristics can be used. By varying the autecological characteristics of selected individuals, the viability of different reintroduction scenarios can be evaluated.

One of the critical issues for panther survival is the impact of inbreeding in the small existing population. Much is known about the genetic makeup of individual Florida panthers and the distribution of traits such as cryptorchidism in the population. Since each panther is simulated throughout its lifespan, the model also has the capability to include genetic markers to simulate hereditary phenomena for either the existing or hypothetical populations. Reproductive histories of individuals, including family trees of relationships, can also be traced and saved for later analysis.

The panther submodel is coupled to the hydrology submodel, which provides water depths, to the vegetation submodel, which provides cover, and to the individual-based

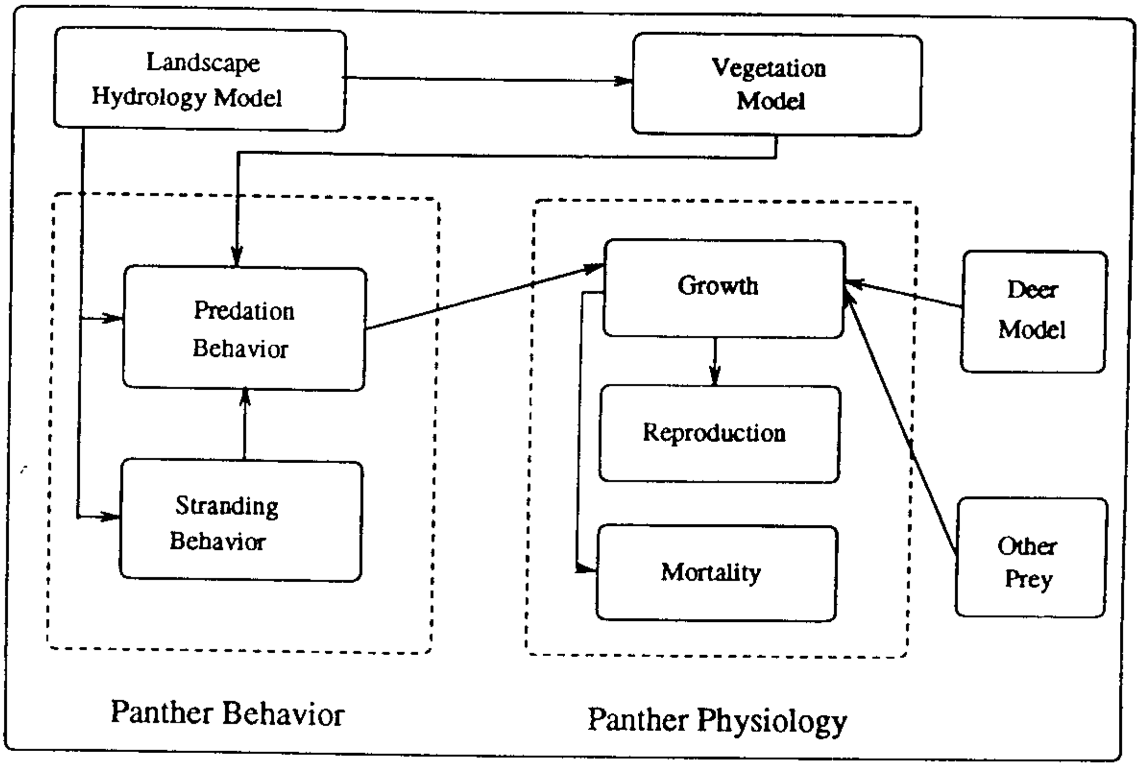

Figure 3: Structure of Panther Component of Deer-Panther Model

deer submodel, which provides prey (Figure 3). Panther behavior and physiology are simulated on a daily time step. Each panther is assigned a state which includes individual characteristics, such as age, sex and weight; predation information, such as number of days at a deer kill site and number of days since the last deer kill; and several sex-specific variables which describe each individual's reproductive status.

Panthers move daily on the landscape at the 500-m scale of resolution, based on behavioral rules which specify:

- short distance local searching for prey.
- intermediate scale and long-distance movement when local searches for prey have failed, with the direction of search depending on the individual's past hunting history.
- remaining at a kill site until the deer has been eaten or has spoiled.
- activity of males in search of a mate.
- dispersal of kittens from the natal range at 18 months of age.

Panthers are limited in their movements and hunting effectiveness by water depth, with different restrictions for males, females, and females with kittens. The maximum distance panthers are allowed to move in a day also differs for each of these categories.

To achieve a realistic distribution of panthers over the study area and simulate social interactions among panthers, the model must incorporate a panther's awareness of the presence and status of other panthers as he moves about on the landscape. This can be done by simulating scent marking by panthers as they move. In the model, each panther marks spatial cells with its unique ID, so that other panthers encountering this mark can identify its sex and reproductive status from the mark. Movement and behavior of each panther is then mediated by the presence or absence of foreign markers. Marks are dated and decrease in potency over time. The incorporation of scent marking in the model structure is currently ongoing.

There are no explicit movement or behaviour rules in the model governing the size or extent of an individual's activity area. Each individual's range arises naturally as the result of scent marking, mating, and predation behavior, which incorporate such factors as panther population density, prey density, topography, hunting effectiveness and mating considerations into the individual's decision-making process.

In simulating predation behavior, the model assumes that individual panthers know where they have been and where they have hunted successfully [5]. By recording for each panther the N-S and E-W offsets from its starting point or center and the location and date of deer sitings and kills, the information needed to incorporate this remembrance of locality into movement behavior is made available. Hunting success is largely a function of prey density, cover type and water depth in the 500-m x 500-m spatial cells. When deer are available, they compose at least 50% of the diet of most Florida panthers [6]. Other prey include feral hogs, armadillos, raccoons, marsh rabbits, and occasionally livestock. A mother with cubs can require as much as 20,000 calories/day. This level of intake can be achieved only when a supply of large animals is available as prey. Panthers relying on smaller prey for food are often unable to obtain sufficient caloric intake to reproduce successfully. The model assumes that, if deer are not found, opportunistic kills of other prey will satisfy the full energy requirements of a panther 40% of the time, with a smaller percentage of energy requirements supplied the remaining 60% of the time.

Each day, the panther's energy balance is calculated to determine whether it gains, maintains, or loses weight. Gain in weight is a function of current panther weight, food intake, and energy expenditures associated with maintenance, travel, predation, and reproduction. Reproductive success depends on stochastic factors and on health of the female, as determined by comparing her present weight with her maximum weight ever attained.

Panther mortality occurs in the model due to starvation, intra-species aggression, accidents, and other factors, such as chemical toxicity and disease. As with deer, starvation is identified by comparing each panther's daily body weight to the maximum weight ever attained, with death occurring when 70% of the maximum body weight is lost. Intra-species aggression is a significant cause of mortality in the South Florida panther population. Panthers fight over territory, since suitable habitat is shrinking. Males also fight over access to females for mating. Quite a few panthers are also killed on highways. Young dispersing males often go through a transient stage before they are able to establish their own territories. During this period their risk of mortality from road hazards and from inter-male aggression is greater than that for older, established males. Spatially-explicit mortality risk from road hazards and from toxicants such as mercury will soon be added to the model.

4 Work in Progress

The model is still under development. The following capabilities are either currently being incorporated or will be added in the near future:

1. A spatial map layer representing regional boundaries for the public lands in the study area is being added, so input parameters and outputs can be categorized by major regions in the study area. This will facilitate the inclusion of factors such as region-specific management practices, hunting regulations, and prey habitat enhancement.

2. A land use map is being added to complement the habitat and regional information, so areas can be identified as agricultural, ranchland, disturbed land, etc.

3. A highway map overlay for spatially-explicit estimation of road hazards for both deer and panthers is being added.

4. Using information from these new spatial map layers, more spatially-explicit habitat preferences and restrictions for deer and panthers can be included.

5. A 100-m pseudo-elevation map is being created for estimating 100-m resolution water depths. This will replace the relative method currently used.

6. The model's capability to evaluate the effects of short-term disturbances such as fire and hurricanes will be further developed and enhanced.

7. Spatially explicit information on distribution of toxicants such as mercury, which affect panther health and mortality will also be added and coupled to a submodel to analyze toxicant effects on individuals.

8. The model is also being parallelized on the CM-5 and the MasPar MP-2 in order to decrease execution time and to investigate general issues involved in parallelization of individual-based, spatially-explicit models.

The Deer-Panther Model is constructed in a flexible format so that results of ongoing research into deer and panther ecology and behavior can be readily incorporated.

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References

[1] Fennema, R.J., C.J. Neidrauer, R.A. Johnson, W.A. Perkins, and T.K. MacVicar. A computer model to simulate Everglades hydrology. In S.M. Davis and J.C. Ogden, editors, *Everglades: the Ecosystem and its Restoration.* St. Lucie Press, Delray Beach, Florida, 1994.

[2] Fleming, D.M., D.L. DeAngelis, L.J. Gross, R.E. Ulanowicz, W.F. Wolff, W.F. Loftus, and M.A. Huston. *ATLSS: Across-Trophic-Level System Simulation for the Everglades and Big Cypress Swamp.* National Biological Survey, ATLSS Workshop, Homestead, Florida, June 1994.

[3] Gunderson, L.H. Vegetation of the Everglades: determinants of community composition. In S.M. Davis and J.C. Ogden, editors, *Everglades: the Ecosystem and its Restoration.* St. Lucie Press, Delray Beach, Florida, 1994.

[4] Harlow, R.F. and F.K. Jones, Jr. The white-tailed deer in Florida. Technical Report 9, Florida Game and Fresh Water Fish Commission, Tallahassee, 1965.

[5] Seidensticker, J.C., M.G. Hornocker, W.V. Wiles, and J.P. Messick. Mountain lion social organization in the Idaho Primitive Area. *Wildlife Monographs*, (No. 35), December 1973.

[6] Smith, T.R. and O.L. Bass, Jr. Landscape, white-tailed deer, and the distribution of Florida panthers in the Everglades. In S.M. Davis and J.C. Ogden, editors, *Everglades: the Ecosystem and its Restoration.* St. Lucie Press, Delray Beach, Florida, 1994.