To the Graduate Council:

I am submitting herewith a dissertation written by Yiannis G. Matsinos entitled "Individual Based Models Of Avian Wildlife Populations". I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

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INDIVIDUAL BASED MODELS OF AVIAN WILDLIFE POPULATIONS

A Dissertation
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Degree
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Yiannis G. Matsinos
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DEDICATION

Στους Γονεις μου.

Στην Ξενια.

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ABSTRACT

An individual-based simulation modeling approach was used in an effort to predict reproductive success of two species of colonially nesting wading birds: the Great Blue Heron (Ardea herodias) and the Wood Stork (Mycteria americana). Two totally different problems were looked upon using the approach.

First, the effects of the alteration of foraging conditions for the two species in the Everglades area were considered. The models used for each species followed simultaneously daily activities of individual birds, their spatial movements, foraging efficiency, bioenergetics and growth of the nestlings during a nesting season. For each of the models the effects of reversals were looked upon (that is, increases in depth during the dry season when water levels are normally falling) as a factor affecting reproductive success. Species-specific differences such as visual feeding (for the Great Blue Heron) and tactile feeding (for the Wood Stork were implemented in the models. Simulation results showed that the Wood Storks, frequently foraging in groups, were more affected by the introduced resource scarcity, mainly because of rapid depletion of concentrated resources.

Second, the effects of PCB bioaccumulation were studied in a colony of Great Blue Herons. The model considered spatial

distributions of PCBs in fish in the colony area. Individual birds were followed and their PCB uptake, bioaccumulation, and retention were modeled. Behavioral responses (foraging deficiency, flight speed) were taking into account using dose-response functions. Simulation results showed that the sublethal behavioral responses in many cases can determine the success of the colony.

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PART I

INTRODUCTION

A. OVERVIEW: A HISTORICAL PERSPECTIVE

All things are ordered together somehow, but not all alike, both fishes and fowls and plants; and the world is not such that one thing has nothing to do with another, but they are connected.

ARISTOTLE, METAPHYSICS

The concept of the subtle interconnectedness and the notion of an "order" of biological populations as referred by one of the greatest thinkers of all times is the most fundamental of the questions upon which Ecology as a science has its foundations. As the science progresses we find not only that these interconnections exist, but also that we, humans, only because of our position in that order, can actively make these interconnections and their implied dependencies more and more fragile. Rather than going to an extensive list of anthropogenic interventions and their implied catastrophes we simply point out that, in some cases, though not all, processes can be reversed and trends in nature can be restored to the pre-intervention levels. In that perspective, in pursuit of insight about how processes originate and develop, and how they affect populations, ecologists have acknowledged along with experimentation the role of mathematical modeling as an alternative means for testing hypotheses.

Ecologists have long been interested in factors affecting population dynamics. Attempts were made early in the study of population ecology to use mathematical models in the form of systems of differential equations (e.g. logistic, Lotka-Volterra) to describe individual and interacting populations. These models provided valuable insight about density dependent factors (responsible for stasis, stable cycles, or even chaos). Nevertheless, they were criticized for oversimplifying assumptions, such as, for example, the assumption that the differences among individuals make no difference to the overall dynamics of the population, or, the assumption of complete mixing among individuals (e. g. each individual is equally affected by all others).

It then became obvious that any serious attempt to characterize population growth should take into account factors like the age or size structure of the population, since the dependence of both fecundity and mortality on age and size is high. Leslie was among the first (the same idea was suggested by Bernadelli (1941), and Lewis (1945), working independently) to incorporate age structure using a conceptually simple matrix model to project all the important demographic characteristics of a population, like the stable age distribution, time to approach that distribution, and the rate of population increase for any initial age distribution (Leslie, 1945). His method gained extreme popularity, partly

because of its direct applicability to field or laboratory data in the form of basic life tables. These models showed the stabilizing effects (by spreading and thus weakening perturbations over many cohorts) and destabilizing effects (introducing time lags) on population dynamics (Nisbet et al. 1982).

It is a common belief that is not possible to obtain complete information about a natural population. Since biological entities do not function as physical entities, governed by well-defined sets of rules and principles, we cannot expect that a deterministic model will capture the complete behavior of a natural population.

Starting from the opposing to the deterministic view, namely the view that populations are subject to stochasticity, probabilistic or stochastic models have also been used. They were introduced as early as the 1920's, (Yule, 1924, Furry, 1937), and include two kinds of models. First, there are mathematical models, where the processes are modeled using equations. These include simple birth and death models (Feller, 1939), Markov chains (Bailey, 1964) and Stochastic Differential Equation models (May, 1974). One of the shortcomings of the approach is the fact that even simple model formulations are mathematically intractable concerning solutions in closed form.

Second, there are models using the Monte Carlo Method to introduce some variability in their parameters. This method produces random numbers that have a probability distribution function (e. g. normal, exponential) and uses them to simulate variability in some part of the model (which could be deterministic, too) A fundamental assumption for the use of stochastic models is the lack of information about the actions of certain forces.

B. THE NEED FOR THE INDIVIDUAL-BASED APPROACH

Ecologists have long been interested in the responses of populations to patchy environments. Most mobile animal populations inhabit a variety of habitat types, at any given time, even within a relatively small region. Individuals may have different chances for survival or reproduction, simply because of their location. Spatial heterogeneity affects resources, which in turn affect consumer populations. Foraging theory (Stephens and Krebs, 1986) suggests that foraging individuals respond differently to various resource distributions. Mathematical models with a few exceptions (Okubo, 1980) have neglected the role of spatial heterogeneity on population dynamics.

Recently there has been an increased use of a new type of models, called "Individual Based Models" that have been applied to a variety of individual organisms (fish, mammals,

birds, plants). These are computer models that simulate and follow individual organisms separately, rather than lumping them into classes based on some common property. The actions of each individual (foraging, social interactions) are modeled with the aid of rules and/or equations. Differences among individuals regarding physiological or behavioral attributes are implemented in a straightforward way, by defining variables for each individual and updating them based on the actions of the individuals, throughout the course of a simulation. The approach yields population level dynamics by integrating over individuals. Their emergence has to do with the inadequacy of traditional state-variable models (i. e. models that subdivide populations to different classes of individuals based on their common "state") to yield reliable predictions for certain types of questions. In most cases these models are spatially explicit, so one can incorporate a variety of organismal responses to the spatially heterogeneous landscapes. (Roese et al., 1991, Turner et al. 1994)

In this work I have used the individual-based approach in an effort to:

(i) assess the influence of spatial heterogeneity in resources to the reproductive success of wading bird species, each employing different foraging strategies.

(ii) assess the role of indirect effects caused by bioaccumulation of a contaminant on a wading bird colony.

In Part II of the dissertation I give an overview of the strengths and weaknesses of the individual-based approach. A synoptic review of the areas that the models have been applied is provided.

C. USING THE INDIVIDUAL-BASED APPROACH IN CONSERVATION

In case of small populations, chance effects affecting survival and reproduction of individuals become significant in terms of the overall population. To distinguish between chance events from within the population and events caused by random variations in conditions of the habitat we use the terms:

(i) Demographic stochasticity, referring to random variation in mortality and survivorship caused by chance events caused by individuals.

(ii) Environmental stochasticity; that is, random variation in habitat conditions.

The implication of both environmental and demographic stochasticities is that extinction is always an event with a positive probability in the space of all possible outcomes, so there is always the "risk" of extinction. The allowable size of that risk is a question of politics, not science.

In conservation biology, the concept of risk is expressed in the notion of Minimal Viable Populations (MVP) (Shaffer, 1981, Soulé, 1986). This is defined as the smallest isolated population having a 99% chance of survival for 1,000 years. Individual-based models can offer valuable insight assuming they have the following objectives:

(i) understanding the landscape-, population-, and individual-level processes that influence the number and distribution of animals in space and time, and

(ii) forecasting the effects of management or other human activities on population abundance and distribution.

They can provide with quantitative statements about the populations in concern. Moreover, based on demographic data, they aid in making predictions, and in shedding insight into long-term population trends. These models can by no means be used as recipes for biological conservation; the detailed mechanisms, and processes leading to extinction are too complex, and models are not capable of simulating all the details. Hence, realistically, what modeling can offer is to give a statistical picture of the possible effects of alternative scenarios for the conservation of populations, by describing in the form of probability distributions the projected population trends under each scenario. They can help identifying key factors of risk and responses of

populations to perturbations. For the survival or extinction of populations only probabilistic statements can be made. This is clear since the influences that play the predominant role in population success, like environmental fluctuations, variability of individuals, and rare catastrophic effects have large components.

In conservation biology one is interested in protecting not only endangered species, but also habitat types that support biologically diverse communities. In many cases bird populations, occupying critical positions in the food chain, can serve as indicators of habitat quality, so their conservation, apart from aesthetic reasons, has to do with the conservation of their habitat. The choice of birds as the basis of population models is also favored by the researchers' ability to relate population vitality to reproduction parameters, like clutch size, egg quality, number of hatchlings, number of fledlings and so forth, parameters easily quantifiable and directly able to be incorporated in population models. Wading birds were among the first to receive attention in the case of the Everglades natural system, since the effects of man-driven habitat alterations became caused declines in populations of several species. The problem of habitat loss for the Everglades wading birds is analyzed in Parts III and IV, where colony models for Wood Storks and Great Blue Herons explore the

sensitivity of reproductive performance to an altered hydrological scenario.

In Part III, following an introduction of the approach and its applicability on biological conservation in general, I describe long term dynamics of a colony of Wood Storks in a number of special cases regarding their habitat quality.

In part IV I examine a case study: the role of foraging modes as a factor of colony success for the species of Great Blue Heron and Wood Stork in an unpredictable (and unfavorable) environment.

D. USING THE APPROACH IN WILDLIFE TOXICOLOGY

Numerous models have been developed to characterize the fate of aquatic populations (Barnthouse et al, 1990); fewer have been developed for terrestrial species (Emlen, 1989).Most models of terrestrial populations have management purposes (or harvesting), with few aiming at predictions from the release of chemicals. The purpose of avian and mammalian models is to assess or predict the effect of a disturbance (usually the release of a toxicant) on a relevant population endpoint such as population density.

The focus on birds has three advantages: they are among the best studied groups of animals with easily identifiable life stages, and as relatively large organisms, they can help as

target species for the conservation of whole ecosystems, and finally because of their high societal value they can help as sentinels of ecosystem degradation. As environmental regulators have been asked to determine the probable effects of pesticides and other chemicals on wildlife populations, the need for environmentally realistic population models has become apparent.

In Part V I give an example of how we can assess the risk of colony contamination with the aid of a model of a single colony of Great Blue Herons.

E. VALIDITY AND VERIFICATION OF MODELS

Simulation models (Swartzman et al., 1987) consist of a collection of hypotheses about implementing ecological processes, either in equation form or as a set of rules, in a decision tree, describing how the major elements of the model, that is represented by state variables change over time. Most simulation models are mechanistic, in the sense that the processes they simulate consist of a number of underlying mechanisms, which to our knowledge are responsible for the way the processes occur. This attribute, together with the structures describing the landscape and a variety of model components describing individuals and their behavior increase the complexity of models. Issues of model verification or validation then come into play.

Models can corroborate a hypothesis by offering evidence to strengthen what may be already established through other means(Oreskes et al. 1994). When the issue of model verification and validation is raised, we should keep in mind that we are dealing with a non-closed natural system and our simulations are not replicable. Models can only be partially confirmed by the demonstration of an agreement between observation and prediction. Field or laboratory experimentation provides a means for model confirmation. But no matter how many confirming observations we have, all conclusions drawn by them, would still lead us to the fallacy of affirming the consequent (Ayer, 1959). There always be a possibility that in spite of our data the theory that explains it might not be unique (a straightforward example to this is the Ptolemaic astronomy,totally confirmed for centuries, that was overturned completely by the Copernican revolution). (Kuhn, 1957) Models can only be evaluated in relative terms, and their predictive power is always open to question. We should not forget their heuristic nature.

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PART II

THE STRENGTHS AND WEAKNESSES OF INDIVIDUAL-BASED MODELS

One of the most important problems in the application of modeling to field research and experimentation in ecology is that it requires a variety of simplifying assumptions that often are not compatible with the reality of the biological system concerned. Classical models in ecology from simple population growth, and species interactions (Lotka-Volterra), to complex ecosystem processes, are population based; i.e., they assume that all individuals are the same and therefore they can be lumped together. This approach contrasts with the simple biological principle stating that individuals differ in behavior and physiology, due to a unique combination of hereditary and environmental factors. Most models also fail to distinguish among spatial effects on individuals; they assume that the effect of one individual on another is the same, without taking into account their proximity. They fail to account for the fact that all the interactions within and among populations in nature are inherently local. An individual organism usually affects and is affected by other individuals that it comes into contact with. Despite these problems, state-variable models still remain the principal modeling tools (as far as total number) in ecology.

These problems have been acknowledged by ecologists for decades but until the last twenty years there had not been any alternatives to using state-variable models. In response

to this inadequacy of the models to deal with differences at the individual level and to take into account explicit spatial structures, two new modeling approaches, both referred to as individual-based modeling (IBM) have been proposed: age or size-structured models, referred to as *i*-state distribution models (Caswell, 1988, Metz and Diekmann, 1986) assuming that individuals in some state *i* can be lumped into a single cohort , and computer models following individual organisms separately, or simulation models, referred to as the *i*-state configuration models .

The *i*-state distribution models assume that the characteristics of a population are taken from a (usually continuous, except for Leslie type of models) distribution. Among the *i*-state models, age-structured populations are usually modeled using a McKendrick-von Foerster partial differential equation, and size structured populations with a Sinko-Streifer partial differential equation. The *i*-state configuration models do not assume continuity in the characteristics of individuals; they simulate many different individuals, each with its unique characteristics simultaneously.

The rapid increase, during the last decade, in the computational capacity of machines has played a major role in the development of these models, so more computer models have

been developed capable of following individuals, rather than classes, within populations.

Individual-based models have been developed for a variety of biological organisms (for a review see Huston et al., 1988). There is indeed a striking similarity between the population-level patterns produced by individual-based models of competing plants and by IBMs of trophic interactions in animals. It results from the fact that in both groups an individual responds to the specific level of resources that it actually encounters in its immediate environment. For plants, the level of light, water and nutrients are directly influenced by the neighboring plants, as well as by physical forces that add some stochasticity. For animals, the levels of food an individual encounters are influenced by physical factors, the effect of other animals and a large component of spatial and temporal randomness, resulting from searching behavior.

For the majority of population-based models feeding is treated as a continuous process, the rate of which is determined by the densities of the resource and the consumer populations. From the individual's point of view this is an unrealistic assumption since feeding happens in a discrete manner which depends highly on the underlying spatial distributions, the degree of vulnerability of the resource (prey), and on searching and feeding habits of the consumer.

The stochasticity introduced with these interactions and the variation among individuals result in consequences at the population level that are different from results predicted by population based models. As Stephens and Charnov (1982) stated, individuals respond not only to means, but also to variances. Even the simple models developed so far reveal that trophic dynamics on the population level cannot always be understood without detailed consideration of feeding interactions at the level of the individual.

One of the powerful aspects of IBMs is that they integrate many different levels in the traditional hierarchy of ecological processes. Each level of organization has traditionally been treated as a separate field (e.g. physiological ecology, behavioral ecology, autecology, population ecology, community ecology and ecosystem ecology). Each field has its own phenomena to explain, and most have their own distinctive types of models. IBMs demonstrate the powerful alternative that all levels of this hierarchy can be understood in the context of the interactions between individuals both directly and indirectly, through their effect on the environment (Huston et al., 1988). The individual-based approach in ecology can be regarded as an application of reductionist methodology (Lomnicki, 1988), i.e. deriving the properties of a system from the properties and interrelations among elements of the system. However

certain difficulties arise, both of experimental and of mathematical nature. Large ecological units like forests, lakes, or seas are very complex systems. It seems virtually impossible to identify all the elements of such a system including the interrelations among them.

A more practical problem is how to estimate resource partitioning within a natural population. This can be easily done for a single isolated individual, as well as for a group of plants, or animals kept in a laboratory. However it is often very difficult to find out the resource intake of a particular individual in the field. The large amount of data required to parameterize and test IBMs is of concern at all scales, though particularly difficult to obtain above the population level. These data requirements, although a significant obstacle in the development and use of these models, can also be a stimulant to the collection of appropriate ecological data. The process of model construction can lead to a more efficient data collection. They can motivate people to collect data on individuals, something which has been difficult in some areas.

One of the apparent drawbacks of this approach is that in an effort to achieve generality, one needs to develop new individual-based models for every species-environment combination under investigation. However, since in most situations the growth and reproduction rates are determined

by energetic requirements, modeled usually with a set of rules for allocating assimilated energy for them, we expect similarities in the set of these rules in similar organisms. In addition, experience gained with modeling one species can be useful even when working with a very different one. As an example, many features of an individual Daphnia model (Gurney et al., 1990) have been used for a model of growth and reproduction of marine mussels (Ross and Nisbet, 1991).

Parameters of population-based models (like the competition coefficient in the Lotka-Volterra model) are often highly abstracted, they do not correspond to well-defined and measurable biological quantities, and they cannot be reliably estimated in any particular ecological system. Ecological theory should be both testable and general although these two properties are often incompatible. Aggregation of individuals into large-scale population variables often hides mechanisms and variability at the level of individual interactions that are crucial to the larger-scale behavior of the models.

Simulation IBMs generally follow many individuals through time and /or space, thereby generating large amounts of information (model "data") that need to be adequately summarized and visualized. How should the large amounts of model data be aggregated and summarized into easily interpretable metrics that capture the important features of

the results? Software and hardware currently available are adequate to perform the required number crunching and graphical display of model results. Deciding on what outputs to use and how to summarize the extensive model data generated, however, is an open-ended issue and deserves more attention. IBM developers need to borrow approaches, concepts and techniques from other fields, such as pattern recognition and spatial statistics.

A very important feature of the IBMs is their ability to make connections between phenomena at different scales of biological organization e.g. elucidating the consequences of individual growth to population and community levels. Such organizational levels do not scale up in an obvious way in ecology. IBMs offer a conceptually appealing approach to link the individual level to that of the population and community.

An additional advantage is that they can be used more realistically to analyze questions associated with small population sizes and demographic stochasticity. As a corollary of this point it can often be the case that relatively few atypical individuals can have disproportional effects on a system, and an IBM is the effective tool to discover and examine these effects that aggregated models are incapable to examine. In conservation biology, models are used to manage very rare species for which there are often very detailed data on the few remaining individuals (often in

zoos). These details include specific genetic information, as well as past matings.

IBMs offer an excellent potential to answer questions of natural selection and evolution. Their value resides on the fact that the models are constructed at the level (individual) that selection operates. It would be straightforward to build genetics into simulation IBMs (given the necessary parameter information) and use them to explore the natural selection consequences of multispecies interactions. This has already been well established for analytic IBMs of age-structured populations.

Another key advantage particularly to *i*-space configuration models is that they inherently provide output in the form of probability distributions, and thus predictions can be interpreted in a risk-analysis format. This advantage may be useful to illustrate to managers the nature of our inability to predict deterministic outcomes in real situations.

Concluding, we must agree that whether or not the IBM approach is needed clearly depends on the question posed by the investigator, and the tradeoffs involved between complexity of the models and the intensive data requirements. We need to improve our knowledge in identifying critical aspects of various interactions, and subsequently simplify the models to allow more effective or analytically tractable

exploration. It is hypothesized that generally a small subset of interactions drive major patterns and once these are identified the models will simplify significantly. Clearly we need more studies like those by[11] that collect data so that predictions can be made with both aggregated and IBMs to see if and under what conditions we need to be concerned with following individuals given the nature of the system and the questions asked.

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PART III

CAN INDIVIDUAL-BASED MODELS YIELD RELIABLE ASSESSMENTS OF POPULATION VARIABILITY?

A. INTRODUCTION

There is growing recognition that understanding and predicting the viability of a population of organisms requires representing the dynamics of the population explicitly in a landscape. The resources and other factors that affect a population (predators, refuge areas, etc.) are patchily distributed, so that the individuals may have to use large portions of a landscape over their lifetimes. Time and energy costs are involved in individual movement and exploitation of resources. Also, a population as a whole spread over a heterogeneous spatial area may actually be quite healthy in some areas of the landscape even if it is in decline in certain other places at certain times (e. g. Pulliam 1988, Lewin 1989). Therefore the population over its whole heterogeneous landscape must be considered.

One of the most important problems in the application of modeling to field research and experimentation in ecology is that it requires a variety of simplifying assumptions that often are not compatible with the reality of the biological system concerned. Classical models in ecology, from simple population growth, and species interactions (Lotka-Volterra), to complex ecosystem processes, are population based, i.e. they assume that all individuals are the same and therefore

they can be lumped together. This approach contrasts with the simple biological principle stating that individuals differ in behavior and physiology, due to a unique combination of hereditary and environmental factors. Most models also fail to distinguish among spatial effects on individuals; they implicitly assume that the effect of one individual on another is the same, regardless of the individual in question and what the relative locations are. They fail to account for the fact that most of the interactions within and among populations in nature are inherently local. Except for situations of diffuse exploitation competition an individual organism affects and is affected only by other individuals that come to contact with it. Despite these problems, state-variable models still remain (numerically) the principal modeling tools in ecology.

An Example: Feeding Of Animals

For the majority of population-based models feeding is treated as a continuous process, the rate of which is determined by the densities of the resource and the consumer populations. From the individual's point of view this is an unrealistic assumption since feeding happens in a discrete manner which depends strongly on the underlying spatial distributions, the degree of vulnerability of the resource (prey), and the searching and feeding habits of the consumer. The stochasticity introduced with these interactions and the

variation among individuals result in consequences at the population level that are different from results predicted by population based models. As Lomnicki (1988), stated, individuals respond not only to means, but also to variances. Even the simple models developed so far reveal that trophic dynamics on the population level cannot always be understood without detailed consideration of feeding interactions at the level of the individual.

The viability of a small population may also depend on the detailed structure of the population through time; age and size structure, sex ratio, physiological conditions of the organisms in the population, genetic variability, and so forth. Traditional abstract models for population viability cannot take into account the detailed characteristics of individuals that may be critical to the survival of a small population. Their predictions of extinction are based on abstract mathematical probabilities.

B. FROM POPULATION TO INDIVIDUAL MODELS

These problems have been acknowledged by ecologists for decades but until recent years there had not been any practical alternatives to using state-variable models in animal population modeling. Demographic models describe population dynamics in terms of the numbers of the individuals in categories defined by their individual

characteristics. Age or size structured models like the Leslie matrices, McKendrick-Von Foerster equation, or the renewal equation of Lotka are the most commonly used demographic models that aggregate individuals into classes. Demographic models rely on one common assumption: that individuals experience the same environment, known as the "mixing assumption".

Individuals are characterized by their states such as age or size (i-states by Metz and Diekmann, 1986). Individuals with the same characteristics are classed into the same i-state, and each i-state changes in response to its previous values and its environment The population's state, total population size or structure (the p-state), is given by integrating over all i-states. So if the i-state is a certain age group, the p-state is the population's age distribution. Distribution models assume that the characteristics of a population are taken from a discrete or continuous distribution; size-structured populations are usually modeled using a continuous distribution model, such as the Sinko-Streifer partial differential equation model.

In cases where the i-state distribution is not adequate to express the population, i.e., when the "mixing" assumption fails, then it may be better to adopt an i-state configuration model. In the i-state configuration models (Caswell and John, 1992) or individual-based models (Huston

et al., 1988), each individual is modeled and described by a set of variables representing its key characteristics. The i-state configuration models do not assume continuity in the characteristics of individuals; they simulate many different individuals, each with its unique characteristics, simultaneously.

Individual-based models can take into account both the whole landscape of a population and the details of its characteristics at an individual level. It is an approach in which the population is explicitly simulated as an assemblage of interacting individuals. The survival, growth, and behavior of each individual in the population (or a representative sample of individuals drawn from a population) are followed simultaneously. A few important general reasons for their use in problems in applied ecology are the following:

(i) Each individual in a real population is unique, differing in its own set of characteristics (age, sex, size, condition, social status, etc.) from all other individuals. This is a result partly of genetic differences and partly of the different experiences (movements across a landscape, encounters with prey and predators, mating, and accidents) of each organism, which are subject to stochasticity.

(ii) Individual organisms are capable of making decisions in movement, foraging, predator avoidance, mating, etc., depending on temporally and spatially varying circumstance.

The rapid increase, during the last decade, in the computational capacity of computers has played a major role in the development of i-state configuration models, so there has been an increase in models developed that are capable of following individuals, rather than classes, of populations.

Individual-based models are often complex, in the sense that they require extensive coding and they usually require much computer power and time, but they may also be conceptually simpler and their complex structure reflects a tradeoff of having fewer constraining assumptions than population-based models.

A Simple Model

Individual based models do not necessarily have to be highly complicated. Here is an example of a model, probably the simplest in ecology; exponential growth.

$$W(t) = W(0)e^{rt}$$

where $W(t)$ describes the body weight at time t, $W(0)$ represents the initial body weight, and r determines the rate of growth. The equation describes quite accurately the

growth of many fast living organisms especially in the very early life stages. Koyama and Kira. (1956) have tried to generate the observed weight distributions by choosing from a normal distribution (instead of considering constant) one or more of the parameters of the previous model. If r differs in each individual, and in the case it is a random variable chosen from a normal distribution, with $W(0)$ the same for all individuals, we can have a skewed distribution for $W(t)$ since it follows a logarithmic normal distribution. That follows since

$$\ln W(t) = \ln W(0) + rt$$

Individual differences between population members can have a large, usually stabilizing effect in overall population dynamics. Body weight is usually easily obtained from a variety of individuals within species and from this we can have an estimate of the individual resource intake, probably the most important individual fitness characteristic. From the observations we notice variation among the individuals that could result from a variety of mechanisms Depending on the organism in question there are several factors responsible for the skewness usually present in most weight distributions: poor resources, size-dependent predation, low quality of food are some of the most common ones; environmental factors and stress from exposure to

contaminants are also among the factors that can be important.

C. BASIC FEATURES OF AN INDIVIDUAL-BASED MODEL

A typical individual-based model consists mainly of:

a set of interacting individuals,

a set of rules that describe how local interactions are implemented,

a physical landscape, including resources.

Each individual is characterized by a set of variables regarding the different i-states (age, size, etc.) and the spatial environment yields another variable, the location of the individual, thus giving the modeler the ability to identify individuals in proximity to each other, and with the model's structure to account for local interactions (e.g. competition for food while in a single cell, the basic spatial unit).

Individual-based models are mechanistic in approach. That means that they use information at the level of the physiology and behavior of individual organisms. In principle, there is no limit to the amount of detail that can be put into the description of how individuals interact with their environment and with other individuals. This makes the

individual-based modeling (IBM) approach especially suitable for species populations where individual organisms have been studied in some detail. (Usually, since complete physiological and behavioral information is seldom available for any species, reasonable estimates must be made, usually from closely related species, for those aspects that are not well known). Sensitivity to a complex array of environmental conditions can be incorporated into individual-based models. This includes stochasticity in environmental conditions on any time scale, since the time steps in an individual are set at whatever size is appropriate to include all important environmental effects on individuals.

The fact that individual-based models consider not only the numbers of organisms in populations but also the condition of the individuals within the population offers a great advantage. There are conceivable cases where population size remains relatively constant through time, but where the conditions of individuals deteriorate. The population may seem healthy from the point of view of numbers alone, but may actually be on the brink of collapse. The health of individuals could deteriorate long before this is manifested in a numerical collapse of the population. Therefore, it is vital to model the condition factors of individuals within the population.

D. INDIVIDUAL-BASED MODELS AND GENETICS

The progress in evolutionary ecology after the introduction of the concept of the evolutionary stable strategy (Maynard Smith, 1982) has been moving towards a rejection of the classic hypothesis of the homogeneity of natural populations, denying that genetically similar individuals living in an identical environment must necessarily exhibit the same behavior. The existence of mixed strategies suggests that not only the mean value of a trait but also its variation can be adaptive.

For example, Bell (1982) considers spatial heterogeneity as the most important factor for the evolution and maintenance of sexuality. However, although traditional concern for threatened and endangered species often focuses on the genetic consequences of small population size, the demographic consequences of habitat loss may be a more important threat for extinctions (Lande, 1988b). Even in cases where extinction is not imminent, demographic consequences seem to play a more important role than genetic ones.

E. INDIVIDUAL-BASED MODELS IN CONSERVATION BIOLOGY

An additional advantage of i-state configuration models is that they can be used more realistically to analyze

questions associated with small population sizes and demographic stochasticity. As a corollary of this point it can often be the case that relatively few atypical individuals can have disproportionate effects on a system, and an IBM is the effective tool to discover and examine these effects that are ignored in aggregated models. In conservation biology, models are used to manage rare species for which there are often detailed data on the few remaining individuals (often in zoos). With an increased emphasis on captive breeding programs zoos can serve as sources of valuable information, including tracking genetic lineages, as well as phenotypic traits (Tangley, 1988).

However, we must make a distinction between the individual-based approach and the widely used population viability analysis. The latter is an extension of demographic analysis lacking a specific methodology or statistical framework (Shaffer, 1990), often taking into account habitat requirements, vulnerable stages in the species life history,that focuses on the ability of a species to persist in an environment (Schaffer, 1991). It usually makes predictions about the mean time for extinction of an abstract population, with little or no emphasis on its ecological characteristics, and without consideration of spatial attributes of the environment.

IBMs offer an excellent potential to answer questions of natural selection and evolution. Their value resides on the fact that the models are constructed at the level (individual) on which selection operates. It would be straightforward to build genetics (Rice, 1984, Heuch, 1978)into simulation IBMs (given the necessary parameter information) and use them to explore the natural selection consequences of multispecies interactions. This has already been well established for analytic IBMs of age-structured populations.

In the field of biological species conservation another important question is how do we assess populations at risk. To be more specific, for each particular conservation problem we need to have a clear idea about the baseline scenario, i.e. what would be the population attributes assuming the absence of such a risk. Is population size, habitat quality, health (fitness status) of each individual, or genetic composition our assessment endpoint? These attributes, although related to each other are not of the same importance in each of our conservation problems. However, starting at the individual level we can answer most of these questions. In cases where processes operate at large spatial scales over long time periods (in some cases we are interested in evolutionary time) the natural way to extrapolate from experiments done at smaller scales over short time periods is

through modeling. This is undoubtedly an economical choice since large scale experiments are not only unreplicable, but expensive as well.

F. A CASE STUDY: WADING BIRDS IN THE EVERGLADES NATIONAL PARK.

In this section we present an example of an individual-based model created to assist in answering questions about the decline of colonially nested wading birds in the Everglades.

Wading bird populations have experienced declines both in population numbers and in reproductive success over the past decades. There have also been a series of concurrent human-dominated landscape changes in the Everglades. A number of alternative hypotheses have been suggested in an effort to explain these declines with two of them seemingly more consistent with observations: (1) The reduction in total size of the Everglades as a result of development and/or overdrainage, resulting in general habitat loss, and (2) An increase in the frequency of major drydown events that leaves insufficient time to prey standing stocks to replenish in the most favorable feeding areas, the short-hydroperiod wetlands, resulting in heavy loss of specific habitat.

The approach taken was to use an individual based model. Wolff (1994) developed the model (a description is given in

Part IV). The endangered species of the Wood Stork (Mycteria americana), was looked upon using an individual-based model of a single colony. The principal parts of the model include (1) a submodel of the spatially heterogeneous landscape, (2) a submodel for the resources (fish prey) which is variable both in time and space, (3) submodels for the behavior of the nesting adults and (4) submodels for the energetics and growth of each nestling, until fledging (or death).

Landscape heterogeneity was taken into account by subdividing a 40x40 km landscape to 25,600 square cells of 250m side each. Each cell had its own average elevation, so that the typical topography of the central part of the southern Everglades was described. In the model the transitions from the wet to dry season were described by the daily water level changes that could take into account rainfall events that can cause reversals during the drying season.

The prey for the wading birds in the Everglades consists primarily of macroinvertebrates and small fish. For long-legged waders a certain water depth range (for Wood storks 10-40 cm) determines which are the most profitable cells in terms of resources. A simulation starts at the end of the wet season, with prey assigned densities that are typical for the hydrological conditions simulated. Background competition for resources from other non-breeding

overwintering species of wading birds is taken into account by partitioning the resources based on local abundances and needs of the competitors. The wading birds feeding in a cell can reduce the fish biomass of that cell. Because their foraging efficiency is proportional to resource levels, it is reduced as resources become scarce. In the absence of foraging birds, fish previously depleted from cells can replenish, provided that the cells are submerged in water.

Behavioral rules and energetics of the nesting adults

A set of rules determines the behaviors of the birds from one time interval to the next. The time step for the simulation is taken to be 15 min., because many discrete activities of the birds like bringing food back to the nest takes as short time intervals. Changes in water depth are daily,however. The first decision made concerns when a pair is ready to begin nesting, strictly based on projecting short time (one week) availability of resources in the vicinity of the colony.

After nesting starts, the decisions made by the adults are guided by various constraints. Each adult must meet an energy maintenance requirement daily. Wading birds can decide whether or not to forage alone, or to join already formed foraging groups. The location chosen by an individual to forage is based on its partial information concerning the

system. It is assumed that each individual has some knowledge, perhaps obtained by visual cues when flying or soaring about the water depths of various locations in its foraging area. However a bird does not know if a cell, chosen for its appropriate water depth, is one that is profitable in resources, so we have the possibility of mistakes.

Example of flocking

An example follows describing the rules of joining a flock: Suppose there are 10 birds foraging at 3 sites, 3 birds at the first, 5 birds at the second, and 2 birds at the third site. If a bird decides to forage at any of these cells it will choose the first with a probability of 3/10, the second with probability of 5/10, and the third with a probability of 2/10. Flocks will thus grow at different rates, with larger flocks growing faster than smaller ones.

If the adult stork finds no prey during the 15 min. interval, it moves to another cell, possibly distant although there are travel costs associated with flying longer distances, where the same rules for joining flocks or not would apply.

The growth of the nestlings is calculated on the basis of the energetic value of the daily allowances in food from their parents. Food requirements for growth and starvation thresholds have been taken into account. For example, if a

nestling does not attain an experimentally set threshold of accumulated food before the rainy season starts or if it receives less than a specified threshold of food over five consecutive days it dies and is removed from the simulation. If the parents will not meet their own energetic needs they will abandon their nest, causing their nestlings to perish.

Extensive simulations have been performed in an effort to examine the causes of decline of the wading birds (Wolff, 1994). Instead of summarizing these results we would like to look at the effects of a single mechanism on colony success. In particular we demonstrate how the model can describe exploitative competition for resources. The relationship between success at the individual level and spatial heterogeneity depends on whether there is scramble or contest competition for resources. It is hypothesized that if each individual is free to exploit all kinds of patches (i.e.there is no territoriality), then spatial heterogeneity should not have an effect on phenotypic variation. However, the above hypothesis seems to be applicable in resource rich environments, where individuals will not have to spend time searching for food. If resources are scarce, then locating profitable patches becomes a stochastic event and even scramble competition can promote variation in individual success.

Altricial nestlings, such as storks, show total dependency on their parents for food for a long period of time. Egg laying (and hatching) is asynchronous and it has been suggested (Fujioka, 1985, Mock, 1987), especially in resource limited situations, that older nestlings have a competitive advantage over their younger siblings. We ran two different scenarios. The first is a resource-unlimited situation and, as fig.1* shows, all nestlings fledge succesfully. In the successful breeding season scenario all 150 nestlings fledge successfully so the probability of success histogram (fig.2) may be trivial. Both contest and scramble competition were implemented but the results were indistinguishable.

In the second scenario we decreased by 30% the initially available resources in an effort to promote the effects of competition. Note however, that in contrast to nestlings, the competition for resources in adults is purely exploitative, i.e. there are not any social dominance structures among them.

The effects are shown in figures 3 and 4. In the 30% reduction of resources case, assuming scramble competition the chronology of birth does not play any role. In the

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* Figures may be found in an Appendix to each part.

probability of success histogram (fig.5) the three categories end up with almost the same * rates (9%, 8%, 10%).

When the older nestling has a competitive advantage over the others then we see the effect of it in the probability of success histogram (fig. 6) where the rates are (70%, 30%, 8%). In the case of contest competition all but two nests (that were deserted) raised one young.

These results are intuitively clear since by modifying the resource allocation rules in the nest we determine who will be a successful fledging. Going a bit further we ask how the availability of resources (as a variable) affects the reproductive success of the colony under either competition scenario. The results show (figures 7,8) threshold effects in fish availability in both cases. In the scramble competition at ~80% of resources all three success curves simultaneously drop with the "1" and "2" curves quite close. This means that in scramble competition, if one nestling fledges successfully the probability that at least one of its siblings is successful is quite high, since there is not any competitive advantage.

In the contest competition case, however, although we still have threshold effects, we notice that if the resources are

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* We have run 50 simulations, probably not enough for the Law of Large Numbers to equate these rates.

abundant, besides their strongest competitor, both its siblings fledge successfully. As the resources become less available the probability of success of "2" and "3" decreases, but still their successes are quite close since they do not differentiate in resource allocation.

In the above example we wanted to compare individual success (as part of colony success) based on the type of competition for resources among nestlings. This helps demonstrate how individual-based models can be used in an effort to identify the determining components, including differences in behavior, and their mutual interdependencies, regarding the success of the colony.

G. SYNOPSIS

There are a number of advantages that an individual-based approach can offer when applied to assessing the prospects for a rare or endangered species.

1. It can incorporate genetic information specific to each organism and follow the genetic structure of the population through time.

2. It provides a model which, with appropriate parameterization of the landscape and prey, is transportable to locations of other populations. This is because it is based on rules of behavior of the species.

3. It can assess alternative restoration scenarios to sustain a viable endangered population over several decades in a spatially explicit manner.

4. It can synthesize previous field work on the species population and its prey and other species it interacts with, including behavioral information.

5. It allows one to conduct model management "experiments" in detail. For example, one could use such models to plan animal releases from a captive breeding program to determine if there are scenarios that provide consistently higher population survival and genetic diversity.

6. It can help identify specific gaps in currently available knowledge of the species to guide future observations.

7. It allows for the inclusion of potential stress factors, such as toxicant exposure in the environment and uptake by means of the addition of a submodel for toxicant uptake for each animal and a submodel for its effects on behavior.

8. Another key advantage particularly to i-space configuration models is that they inherently provide output in the form of probability distributions, and thus predictions can be interpreted in a risk-analysis format. This advantage may be useful to illustrate to managers the

nature of our inability to predict deterministic outcomes in real situations.

In conclusion, we must agree that whether or not the IBM approach is needed clearly depends on the question posed by the investigator, and the tradeoffs involved between complexity of the models and the intensive data requirements. We need to improve our knowledge in identifying critical aspects of various interactions, and subsequently simplify the models to allow more effective or analytically tractable exploration. It is hypothesized that generally a small subset of interactions drive major patterns and once these are identified the models will simplify significantly.

Individual based models can help us answer questions regarding management alternatives, the estimation of minimum viable population on a specific habitat, the design of nature reserves, chances of success for reintroductions and many more.

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APPENDIX

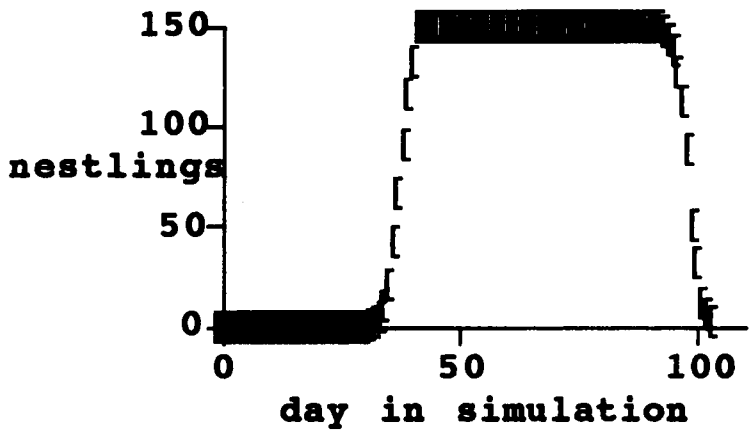

Fig.1. A successful season. Nesting started early (on day 6) and is over before the wet season begins. All nestlings fledge (threshold: 14kg).

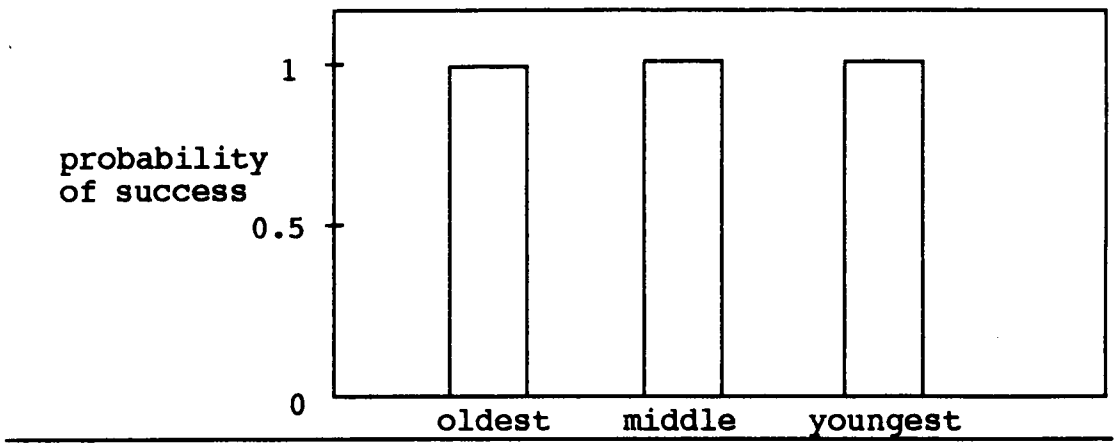

Fig. 2. Probability of fledging for nestlings during a successful breeding season.

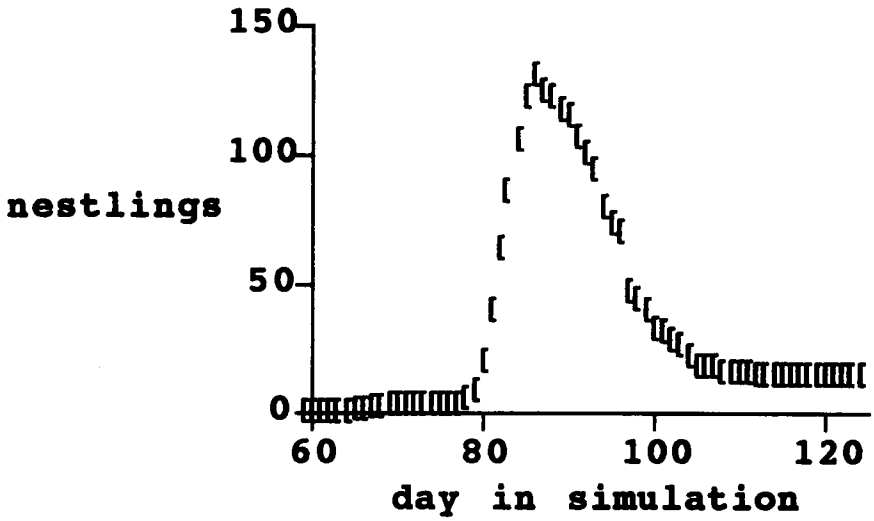

Fig. 3 30% reduced resources-Scramble competition. Nesting is delayed >15 days. Prey availability is insufficient: most nests are deserted (adults cannot satisfy their own energy requirements, nestlings starve). Only 12 nestlings fledge.

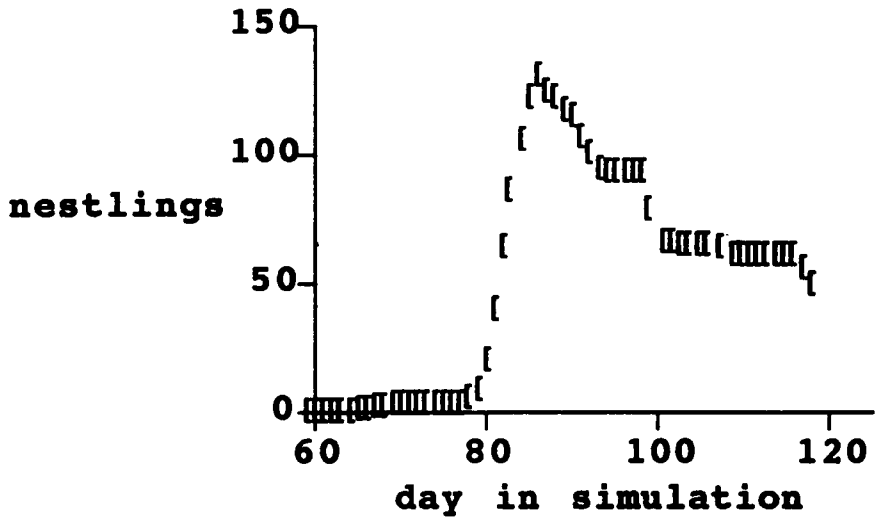

Fig.4. 30% reduced resources-Contest competition. Nesting is delayed >15 days. Prey availability is insufficient: all but two nests raise one young; younger nestlings starve). 54 nestlings fledge.

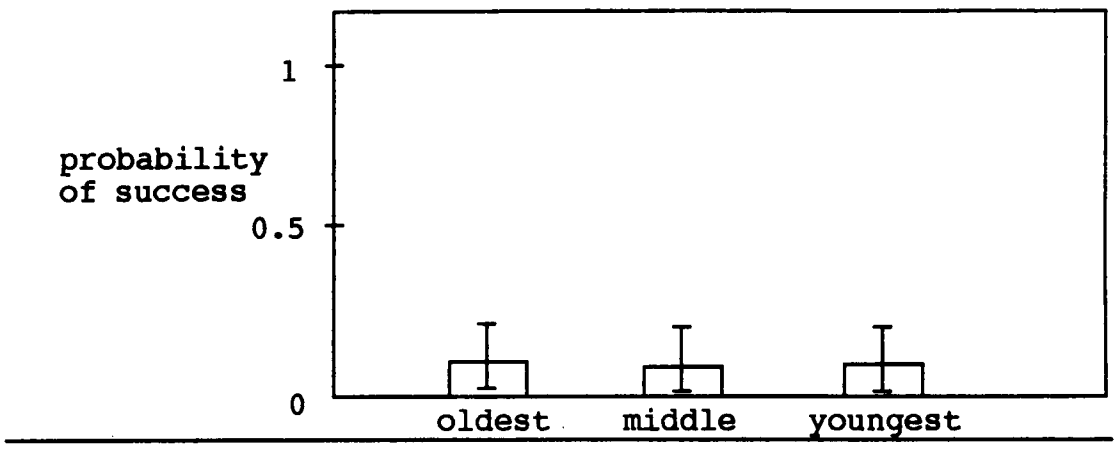

Fig. 5 Probability of sibling success in the 30% reduced resources-Scramble competition

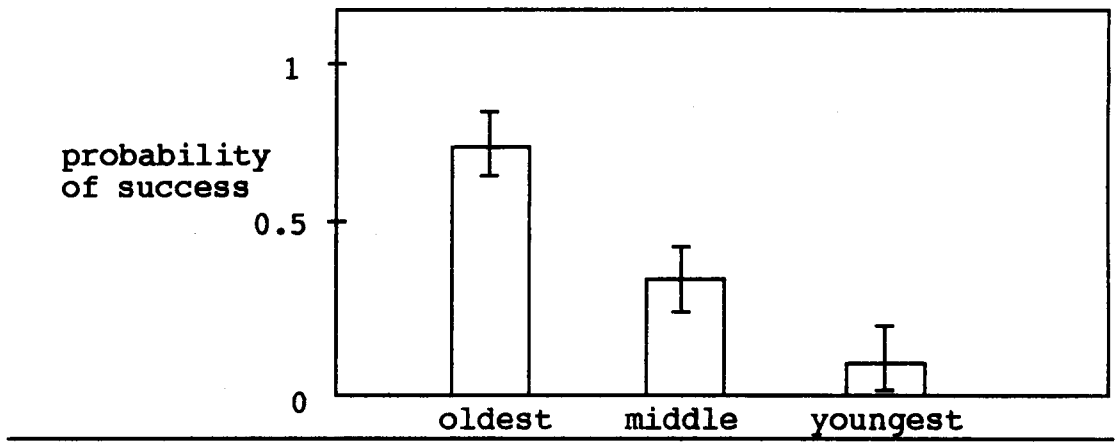

Fig. 6 Probability of sibling success in the 30% reduced resources-Contest competition

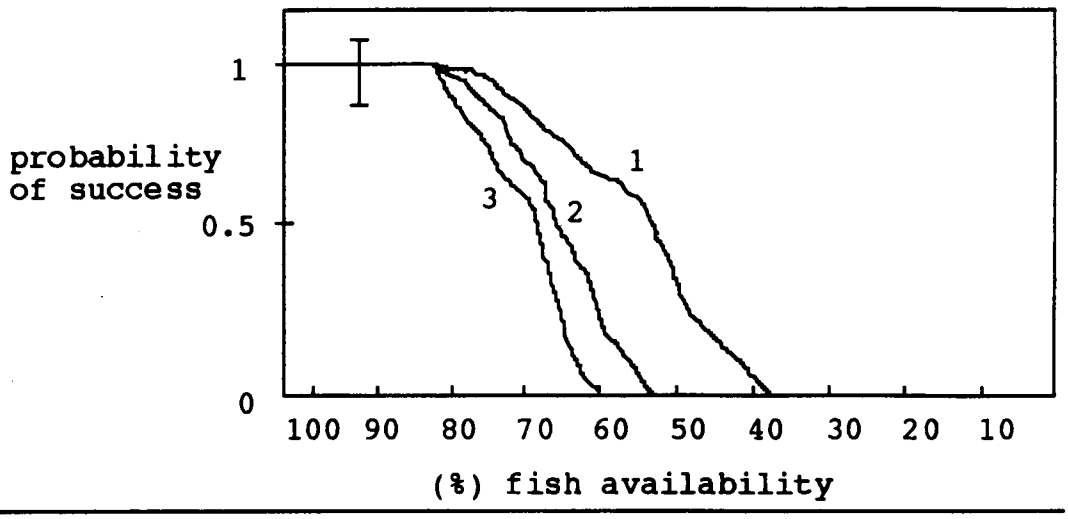

Fig 7 Reproductive performance as a function of resources in the case of scramble competition among nestlings

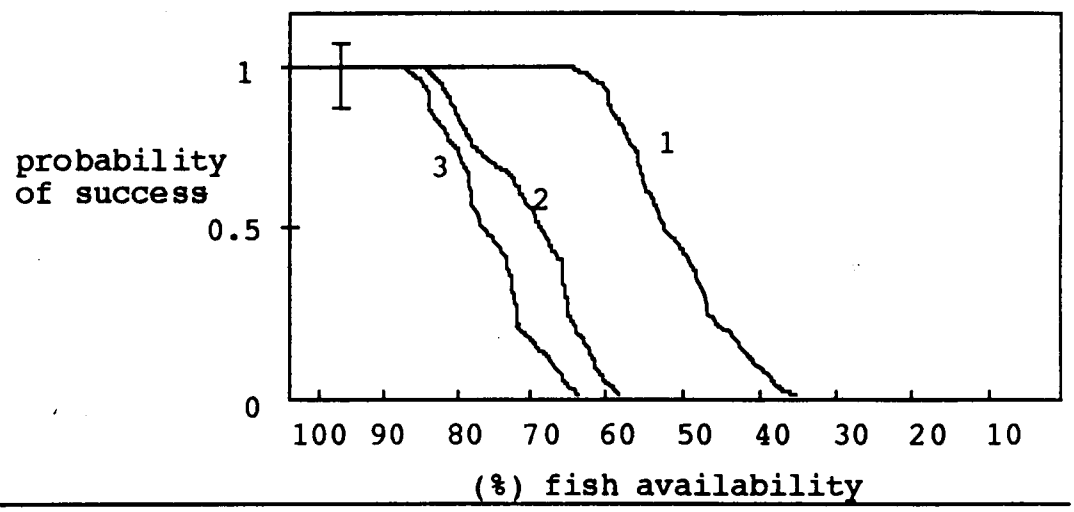

Fig.8. Reproductive performance as a function of resources in the case of contest competition among nestlings

PART IV

ADAPTIVE FORAGING BEHAVIOR IN A HETEROGENEOUS ENVIRONMENT; IMPLICATIONS OF AN INDIVIDUAL-ORIENTED APPROACH FOR WADING BIRDS

A. ABSTRACT

The reproductive success of colonially nesting bird species is sensitive to the availability of resources. In resource-limiting cases it is hypothesized that individuals facing starvation can adapt their foraging behavior to the spatial and temporal heterogeneity of the resources in a number of ways. In an effort to assess the role of adaptive foraging behavior in heterogeneous environments as a factor determining the success of the colony, we used single-colony individual-oriented spatial models for the Great Blue Heron (*Ardea herodias*) and the Wood Stork (*Mycteria americana*). The models followed simultaneously daily activities of individuals, their spatial movements, foraging efficiency, bioenergetics and growth of the nestlings during a nesting season. For each of our 50-pair colonies we used two contrasting scenarios; in the first, the extent and distribution of feeding sites and continuously falling water depths ensured successful reproduction for both species. In the second, we simulated reversals in water depth (that is, increases in depth during the dry season when water levels are normally falling), caused by heavy rainfall.

The results confirm that Wood Storks were significantly more adversely affected than Great Blue Herons by the prey dilution caused by the reversals in water depth. In the latter

scenario where resources became scarce, resource predictability decreased, and the foraging birds tended to form groups, thus minimizing searching time. This led, particularly for the Wood Storks, to rapid prey depletion, and low foraging success, resulting in poor reproductive performance.

KEY WORDS: Wading birds;Great Blue Heron;Ardea herodias;Wood Stork;Mycteria americana;Everglades;foraging behavior;individual-based models.

B. INTRODUCTION

The wading bird community is an important indicator of the health of the Everglades ecosystem. The natural spatial and temporal variability of the ecosystem maintained a high diversity and abundance of wading bird species, which included ten species of egrets and herons, two ibises a spoonbill and a stork (Bancroft et al. 1990). The total populations of wading birds breeding in the Everglades-Big Cypress ecosystem declined from about 2,000,000 individuals in 1870 to about 500,000 individuals in 1910 due to plume hunting of most species (except the Wood Stork). Populations of nesting birds were estimated to be about 250,000 in the 1930s compared with 55,000 during the years 1974 to 1981, and 20,000 to 30,000 since the mid-1980s. (Robertson and Kushlan 1984, Ogden and Johnson, 1990).

Wading bird population decline was concurrent with habitat loss. From 1900 to 1973 the acreage of wetland habitats decreased 35% in the area south of Lake Okeechobee (Browder, 1976). Additionally, the drainage patterns within the Everglades-Big Cypress region were severely altered. Historically, a broad sheet of water flowed south of Lake Okeechobee through the freshwater sawgrass marshes and into the mangrove estuaries. The Everglades typically experience a six-month rainy season from mid-May to early October and a six month dry season from November through April. (Fig. 1) As water levels recede in the dry season, fish become trapped within discrete pools, allowing easy exploitation by wading birds. The nesting cycles of wading birds is timed to coincide with the winter-spring dry season. Currently, however, sheet flow within the Everglades has been dissected and intercepted by more than 2,222 km of canals and levees, disrupting the hydrologic cycle and subsequently the patterns of food availability.

Due to fluctuating weather conditions, nesting populations of many species of wading birds are highly variable. Historically, the nesting colonies of most species of wading birds were concentrated in the mangrove-coastal marsh areas around Shark River Slough. This ecologically productive and topographically complex brackish water area supported abundant populations of small fish, on which wading birds depend for

food. It is generally accepted that the natural hydrologic cycle of summer rains and winter dry-downs functions to first expand fish populations and then concentrate them into shallow waters and isolated pools, facilitating foraging by wading birds during the late winter-early spring nesting season, when energetic demands are the highest. Different species have somewhat different hydroperiod and habitat requirements, and therefore differ to some degree in the location and the timing of nesting and foraging activities. During nesting, most species of wading birds forage within several kilometers of their nest sites and tend to avoid dense grass habitats. Wood Storks, however, which have the longest breeding season, forage up to several tens of kilometers from their nesting sites. Deep pools of water in Shark River Slough formerly maintained a foraging refuge for overwintering birds during periods of extreme drought.

Wading birds can only forage in relatively shallow water. Long-legged feeders (Wood Storks, Great Blue Herons) need water depths between 10-40 cm (Custer and Osborn, 1978, Powell, 1987). Thus, water levels must be below about 40 cm to allow successful foraging. Dropping water levels cause fish to become concentrated in isolated depressions throughout the marsh. Birds effectively exploit these concentrations, usually to depletion. Over the course of the pre-nesting and nesting season, a succession of these fish concentrations must

form as the fish populations of these ephemeral pools are depleted. To make these pools available, a nearly continuous recession of water levels must occur from December through May. Major reversals in this recession, due to heavy rainfall, cause water levels to rise, dispersing fish and making efficient foraging by wading birds more difficult. Stalls in the recession allow wading birds to fish out pools that are at optimal water depths but prevent the formation of new pools. If stalls or reversals persist, nest failures and (if severe) colony abandonments occur (Kushlan et al. 1975, Frederick and Collopy, 1988).

In an effort to identify species-specific responses to variable and unpredictable environments with respect to resources, we chose to simulate nesting cycles of two wading bird species that differ strongly in foraging methods. We simulated a colony of Wood Storks and a colony of Great Blue Herons, species quite similar in their physiological characteristics, life cycles and energetic requirements, yet different in the way they forage, and the kind of food they require.

C. METHODS

Computer simulation modeling provides a tool for performing a large number of numerical (vs. empirical) experiments changing a variety of assumptions in respect to the hypotheses we are

testing. Field experimentation is generally not possible, especially on large scales, where such replication would involve problems not only associated with costs of implementation of actual hydrological scenarios, but also in putting at risk the populations we are interested to conserve. Computer simulation experiments can be used as a surrogate for actual field experiments.

Individual-oriented models (IOM) offer an appropriate framework for incorporating a high degree of realism in simulation modeling, by closely following actions of individual organisms that constitute the biological population of concern. Various behavioral components, such as foraging, social interactions, together with physiological processes, like reproduction and growth, are modeled at the level of the individual organism. Individual-based models have been applied to a variety of ecological problems (Huston et al. 1988, DeAngelis et al. 1992), especially in cases of highly heterogeneous landscapes, or when abiotic factors change constantly. In such cases, models with traditional state-variable based aggregations of individuals make predictions about the average individual, which may not be of use when variability within the population is high, and such average individuals do not exist in reality. There are a number of advantages for using the individual-based approach that include the following:

(i) The inherent variability within populations is incorporated by modeling distinct individuals and thus accounting for their differences both in physiology (e.g. sex, weight, fitness) and behavioral attributes (foraging, social interactions).

(ii) Animal behavior, in particular decision-making, can be described with the aid of a set of behavioral rules based on a decision tree. In this way the actions of an individual can be based on its own particular set of experiences.

(iii) Local interactions can be taken into account. Each individual's spatial location is tracked through time; an individual's fate is affected by other conspecifics that share local resources and information about the location of resources.

(iv) Modeling behavioral attributes suggests a short (as compared to state-variable models) time step of usually less than a day. That is appropriate in capturing short-term environmental fluctuations and stochasticity affecting individuals. State-variable models typically use longer time steps related to the time scale of change of the state variables. Short time steps are easily implemented on high speed computers.

D. DESCRIPTION OF THE MODEL

We use computer models to simulate wading birds during their breeding season. The modeling approach we are using has been described in detail in (Wolff, 1994). The colony model for Wood Storks has been used as a baseline for developing colony models for Great Egret and Great Blue Heron. In the following we give an overview of the basic model components, and where appropriate, distinguish among the specific rules used in each model. Parameter values are given in Table 1.

The models consist primarily of the following parts (submodels):

(i) a spatially explicit landscape submodel, taking into account the hydrological cycles, so cells are characterized by a changing water depth.

(ii) a submodel for prey resources, temporally and spatially dynamic

(iii) submodels accounting for the energetics and behavior of nesting adults, and

(iv) submodels for the growth and energetics of the nestlings, until fledging

Landscape submodel

Landscape heterogeneity is taken into account by considering subdivision of the area surrounding the colony to contiguous spatial square cells, each with its own elevation and water level, so that the main attributes of topography are included for the foraging areas. Further details within each cell, such as vegetation types and alligator holes are not considered. The grain for the above landscape is not the same for the two models; for wood storks the size of the cell is taken to be 250 m x 250 m, and for herons it is reduced to 50 m x 50 m for reasons explained in the following section. In brief, as the dry season progresses, water levels recede, and each individual cell's water depth goes down until completely dry, or, alternatively, until rainfall events reverse the decline. Water levels are updated daily in the model.

Prey base submodel

Wading birds feed primarily on aquatic prey (Hancock and Kushlan, 1984). They stand or wade slowly in shallow water areas and stab, grasp, or filter their prey (Kushlan, 1978). Thus they need not only adequate food supplies, but also appropriate water depths for foraging. Because such suitable foraging conditions are both irregularly distributed and short-lived, these birds have large home ranges and change foraging sites frequently. Successful breeding requires the

continuous availability of profitable foraging locations throughout the entire nesting season. Water conditions can change substantially within a week. This has an effect in the local concentrations of fish and macroinvertebrate populations.

Two factors related to prey are critical to allowing wading birds to nest successfully. First, sufficient biomass of fish must have grown in the marshes over the previous year to provide food for active colonies. Environmental factors that influence reproduction and growth of the major prey species for the heron, *Poecillia latipinna, Fundulus confluentus, Lepomis punctatus, Cyprinodon. variegatus*), will have a major impact on the biomass of prey available to birds. Under favorable environmental conditions these species reproduce and grow rapidly. The marshes must reflood to sufficient depths early in the summer to allow these fish to reproduce and grow rapidly. *Lepomis punctatus* are longer-lived fish than the others and require more time to grow to larger sizes. Loftus and Eklund (1994) have shown that the hydroperiod of a marsh and the length of time between complete "drydowns" are closely correlated to the biomass of fish these marshes support. Marshes must be reflooded relatively deeply and for long periods; however, it is also critical that fish become available to foraging birds in a continuous manner throughout the entire breeding season. Thus, if marshes were flooded

deeper, a "normal" drydown would still provide a "drying edge" (a suitable for foraging moving -as drying progresses- area) are for feeding, but would not completely dry out the deeper sloughs. This would leave a residual fish population to recolonize the marshes when the summer rains begin.

Both models assume fish and aquatic macroinvertebrates as the main food item of wading birds in the Everglades. Due to habitat heterogeneity and dynamically changing water levels, resources are taken into account in a dynamic way. In the beginning of the simulation (near the end of the wet season) fish biomass values typical for the hydrologic conditions being simulated are assigned to all wet cells throughout the landscape. The prey base assigned to each cell is assumed to be accessible to the birds only if water levels are sufficient for wading which differs for different wading bird species. Since the same resources are exploited by other birds than those simulated, often non-breeding, overwintering birds, we have discounted the actual prey base to account for the background competition. Since data on prey availability are quite scarce and not always accurate, cells have been assigned fish densities from different distributions with parameters (means, etc.) estimated from field data. Thus an average of 70 kg/cell is assumed to be available to the foraging birds (Kushlan, 1980). For the Wood Stork model all prey is assumed to occur in the form of Cyprinodontoid and Centrarchid fishes,

with an average weight of 1.73 gr (Ogden et al., 1980). However, visually feeding long-legged waders, like Great Blue Heron, exhibit a much broader range of sizes of consumed prey (Kushlan, 1978). Field data suggest that larger fish like L. punctatus, and smaller, like P. latipinna constitute its diet. The prey base submodel accounts for this. The unit of prey is 20 gr. and the foraging bird can handle prey items of 1-5 units at a time. The choice of 20 gr. as a unit is rather of practical value from a modeling viewpoint. The idea is that within a cell we can specify the size distribution of fish based on the unit as, for example, 20% of size 1 (1 unit), 30% of size 2, 15% of size 3, 15% size 4, and 20% of size 5. Based on these abundances a foraging bird will encounter a fish of size 1 (20 gr.) with a probability of .2, a fish of size 2 (40 gr.) with a probability of .3, and so forth. It is often the case, especially during the dry season, that prey are quickly depleted within a cell when a flock is formed at the cell. Therefore in the model prey abundance is monitored in 15-min intervals. If a cell dries out it is assumed not to be replenished with fish if it becomes wet later in the breeding season. It follows then that the effect of rainfall is to reduce the number of the cells with resources.

Behavior and Energetics of adults

A. Rules pertaining to the Wood Stork Model

Each adult bird's actions (foraging, social behavior) as well as its physiology and energetics, are specified according to a set of rules. These rules determine the status of the adult bird, which is updated every 15 minutes. The time step is chosen to be in agreement with the duration of many discrete activities of the birds, like time required to bring food in the nest, feed nestlings, etc. The very first of the choices that the birds have to make, is when to begin nesting.

The Wood Stork model assumes that if a female is able to forage sufficiently for a week, with resources being able to satisfy a foraging threshold (20% more than its requirement), during the late wet season, nesting will start. Eggs are layed asynchronously, and both parents take turns incubating. Adult Wood Storks are simulated between 10 a.m. and 4 p.m., since foraging trips generally take place between these hours. This is possibly due to the preference Wood Storks show for soaring flight (Kahl, 1964), since they wait to use the thermal updrafts from the colony to the foraging sites and back.

One of the decisions a bird must make before foraging is where and how to forage. It is assumed to have some partial

information about the landscape, so it knows which are cells with appropriate water depths; but it is assumed ignorant of the resource levels in them, so sampling of the cell is required and mistakes are common. The foraging bird can either forage by itself or join a flock already formed. There are, as will be discussed later, certain advantages and disadvantages associated with flocking. A bird deciding to forage alone will search the adjacent cells if the prey abundance in the cell that it is currently in is not adequate. The model assumes that if more than one flock exists in the vicinity of an adult that could potentially join, the decision regarding which flock to join is weighted by the size of the flocks. For example if three flocks, one with 5, one with 3 and on with 2 birds exist, a bird will choose the first with a probability of .5, the second with .3, and the third with .2. Usually the presence of a flock is an indication of high food density; however, since depletion by the flock takes a short time, the benefits of a late joining bird are minimal.

B. Rules pertaining to the Great Blue Heron model

The initiation of the nest is governed by rules similar to those in the previous model. A threshold of 600 kcal for a week is the required energy that a female must obtain in order to start a nest.

Visually feeding long-legged waders exhibit a much broader range of sizes of consumed prey. So it was necessary to change the prey base submodel from that used for Wood Storks. The unit of prey is 20 gr. and the foraging bird can handle prey items of 1-5 units at a time. Size and type of prey determine handling time. Large prey items require more handling, and time increases exponentially with size (Kushlan 1978). Pausing (of foraging) also correlates with size (longer pausing with larger prey items). Prey handling and pausing were implemented in the model in a straightforward way.

Since the actual mechanisms of visual feeding (locating the prey, stalking, and handling) are more subtle than tactolocating (e.g. groping) as it happens to tactile feeders, a significant difference in the foraging success of the young fledglings is observed as compared to their parents.

Environmental factors such as amount and direction of sunlight, wind, etc.(Bovino, 1979), are also factors affecting feeding success. Visual feeders are quite efficient at obtaining prey during the afternoon hours, when the sun is at its peak, and show reduced foraging efforts (not foraging success) during the early morning hours and the late afternoon hours. During the times that the sun is reflected on the body of water with an angle, the birds use alternate foraging modes, like tilting their heads, an adaptation probably to

correct for glaring (Krebs, 1973) or difficulties locating prey caused by refraction of light. Herons usually stalk submerged prey (by a rapid strike), while wading in shallow water. If their eyes are not directly above the prey there is a disparity caused by refraction between the prey's apparent and real position.

Water depth also is an important factor determining feeding success. Herons can forage in shallow water areas mostly on macroinvertbrates, and also in deeper water impoundments on larger prey items, usually mixed with other wading bird species.

In general fledglings are relatively inefficient foragers. Bildstein (1984) found a steady increase in foraging success rates with age in first-year, second-year, and adult white ibises foraging in the same area and at the same time. Similarly, Recher and Recher (1969), and Powell (1978) found that juvenile Little Blue Herons and Great Blue Herons, respectively, had significantly lower foraging success rates than adults. It is likely that young ciconiformes will require excellent foraging conditions to compensate for their developing abilities, perhaps as dense as is required for nesting. Rodgers and Nesbitt (1979) hypothesized that the high development of juvenile heron foraging skills is critical for the survival of young. Very few studies have focused on post-fledging survival, despite the fact that mortality during

this period appears to have a very large effect on recruitment. It seems that an understanding of the factors which affect survival of the juveniles is every bit as important as understanding nesting success.

The model had to be modified based on the above factors, but since the implementation of certain factors (e.g. the effect of cloudiness, or the wind) was far from possible due to the lack of field data, only a subset were implemented as follows:

A bird after locating and landing on a certain cell, will update its feeding capabilities based on:

(i) the depth of the cell

(ii) the actual prey resources of the cell

(iii) the time of the day

(iv) whether the bird is an adult or a fledgling

Two authors (Krebs, 1974, Kushlan, 1976) showed that feeding aggregations of Great Blue Heron *Ardea Herodias* only build up when the prey density is high and birds that forage in groups gain more food simply because flocks form when food is abundant. Solitarily foraging herons quite often establish and defend feeding territories. We changed the cell size to 50m X 50m to account for the fact that visual feeders spend more time searching neighboring sites walking slowly and for

the apparent scarcity of large prey items by increasing the resolution. If resources are abundant then territoriality breaks down and additional birds are allowed to join. This is modeled by the following rule:

Territoriality rule

An adult heron samples a cell. If during the first day it has satisfied all of its energetic needs while in the cell it will return the next day. If this happens for more than one day, other birds searching can join in the cell.

Searching patch rule

Birds are let to forage for a time period of a week. Then an instance variable (its_weekly food), keeping track of accumulated feeding performance, is used at the end of the week for comparison. The birds that fall below the minimum feeding performance are then able to use the upper 20% of the successful birds as information targets. This is implemented as follows:

Before an unsuccessful bird chooses a patch to forage next day, it will decide, based on a probability if it will join other birds, already foraging. Then again it will choose if it will join the "marked" successful birds based on their distance from the bird.

Giving up patch rule

After an adult bird chooses a patch to forage it will stay and feed at the location as long as it is profitable for the bird. If the yield is not sufficient the bird must change feeding locations. The model uses the following rule to determine when a bird will give up its patch:

Assume a bird is at a particular cell for time T . The last feeding occured before time t. Then the probability of giving up its patch will be: $prob[give\_up] = \frac{t}{T}$

Energetics and growth of the nestlings

A. Wood Storks

Adult birds, after satisfying their own energetic needs, must obtain resources for their hatchlings. They regurgitate boluses of the food brought back in the nest, and the nestlings compete for it. The model assumes uneven allocation of the food resources among the nestlings. Usually the oldest chick has a competitive advantage over its siblings, so after it has satisfied its needs the others share the remaining (if any) resources. From experimental measurements, it is known that a nestling must attain a certain threshold level of accumulated food throughout the pre-fledging period in order to fledge successfully. If the adults are not able to provide adequate food supplies before the wet season starts and their foraging efficiency declines, their nestlings are assumed to

die. In addition, the model assumes that nestlings should not be subject to starvation for a prolonged time (3-4 days); otherwise they perish. Nest abandonment is also a possibility in the model, if adults are not able to satisfy their own energetic needs. The model assumes that the minimum total amount of food a nestling wood stork must receive in order to fledge successfully is 14 kg over the nesting period.

B. Great Blue Herons

Every nesting pair lays 3 eggs, asynchronously, with a period of two days between eggs. Each egg is incubated for 28 days before hatching (Palmer, 1962). A nestling fed at the maximal rate can grow at the rate of 40 gr/day reaching a weight of 400 gr. within 10 days, and a maximal weight in ~3 1/2 weeks (Owen, 1960), remains at the maximum for the next two weeks, finally decreasing linearly its daily demands to 150 gr at the final period in the nest.

Each nestling fledges succesfully after 60 days from hatching, if it has accumulated a total of 15 kg of food throughout that period, assuming it has not starved (less than 50% of the accumulated values for a period of 5 consecutive days).

Feeding of the nestlings rule

In herons laying of the eggs is asynchronous, and it enhances asynchronous hatching too. So, on average there is at least a

week of age difference between the older and the youngest sibs. That has been shown to have an effect in partitioning of resources during the nestling stage. So it is assumed that older sibs have a competitive advantage over younger ones during feeding from their parents. This is modeled as follows: depending on the size of the prey that parents bring back to the nest we have the following options: (a) If the adult parent has captured a number of small fish then that is simulated as equal shares for every nestling (scramble competition).

If the catch is one or two larger prey items, then the oldest chick first fulfills its daily energetic requirement, and if the food suffices for the next offspring it will also feed. Since the maximum food that herons can bring back to the nest does not exceed 250 gr., the youngest nestling will necessarily go without food (at least for that particular feeding episode). Thus the model assumes contest competition in the case of larger prey items. Table 1 summarizes the parameters of the Wood Stork and the Great Blue Heron model.

D. SIMULATION RESULTS

Our main objective was to compare foraging modes of a tactile (Wood Stork) to a visual (Great Blue Heron) foraging wading bird species, under normal weather conditions (Scenario 1), and also under reversals of water levels, caused by heavy

rainfall (Scenario 2). The model can provide us with a variety of types of results. Because of its individual-based formulation we can do accurate bookkeeping for a number of distinct individuals on a 15-min step for the whole nesting season. That includes detailed information about the individual's foraging rate in grams/time step, and the fraction of time each bird spends for its daily activities, like flying, searching for food, feeding, feeding its nestlings and so forth. Detailed information is provided in the results for nestlings. Their daily food levels are given, their growth is kept track of, the day for each nestling achieving the threshold for fledging is also recorded. We also can look at resource levels and how they fluctuate temporally and spatially.

From the previous description another significant advantage of the individual-oriented framework emerges: Usually in bird population studies colony success is defined as (i) successful nests/total number of nests, (ii) percent of fledglings/hatchlings, Instead of characterizing colony success by one or two variables, depending on the choice of endpoints, the models provide an array of result types, on individuals, aggregated for the total populations in distribution format. That is of particular use when we compare different colonies' performances, as our results will show.

For our simulations we used a landscape pattern indicative of the topography surrounding colony sites in the Everglades (Fig. 2). The colony is located in the middle of a long-hydroperiod marsh (interior wetland or central slough) surrounded by peripheral wetland areas, which are short-hydroperiod wetlands, areas that because of early drying provide wading birds with sufficient resources in the early nesting period.

We used two different scenarios in our simulations. A total of 100 simulations for each parameter set was performed. In the first the external conditions, particularly the distribution of profitable foraging sites ensure adequate food availability for the breeding birds. The drying cycle is normal and favors colony success (no water level reversals disrupt the food resources). In the second scenario the same parameters are used except for the events of heavy rainfall

Scenario 1. A succesful breeding season

In this scenario both colony models start with favorable water conditions for early nesting. Eggs are laid asynchronously a week after the first pair initiated their nest. Early nesting was commenced before the wet season began (approximately 150 days since the birds arrived at the colony). Food availability was adequate and all nestlings received enough to fledge successfully. After the hatching period as fig. 3

shows (between days 28-32) all nests produced 3 nestlings, so for each species we attain the maximum number of offspring (150). The pattern for both species was similar (fig. 4), with the only difference in the actual duration of incubation which differs on average at 2 days between the two species. Figures 5 and 6 show the accumulated food distributions for the two species. It should be noted however, that although most birds fledged successfully, the distribution of the accumulated food intake shows enough variation among the nestlings to alert us about possible threshold effects concerning our choice of the value that guarantees successful fledging. To this end, the actual distribution of cumulative food intake (rather than just the number of fledglings) may be a better indicator of the colony performance.

In fig. 4 we notice that although the energetic requirements for herons were higher than that for the storks, herons were the first to reach the fledging stage. That is explained by their per capita foraging success. As figures 7 and 8 show, herons tend to spend more time foraging than storks; that compensates for their lower feeding rates compared to storks that spend less time for foraging. As Fig. 7 shows, after nest attendance started, adult birds increased their time foraging by more than 15% on average. This is the high demand period for parents, since the nestlings have hatched and food had to be carried back at the nest. As a result of intensive

foraging, we see that Storks, in particular, tend to form aggregations, thus exploiting resources rapidly and lowering their per capita gain (Fig. 8) . It should be mentioned that according to the rules used by the model regarding foraging behavior and the selection of feeding sites, the birds do not know beforehead the fish abundance of the cells. Since they are biased for choosing cells with flocks already foraging there, they may reduce their foraging rates. The pattern for herons, however does not reflect this phenomenon; it is more like a cyclic (predator-prey) pattern that could account for the short-term memory that the simulated herons have about resources which in their case are quite predictable. The oscillatory behavior could be explained by a time lag between locating cells with prey, passing the information to unsuccessful foragers, and time for prey depletion.

Scenario 2: A breeding season disrupted by reversals

In this scenario the nesting season starts as in the previous scenario, but heavy rainfall during the critical last stages of nest attendance, when the demands for food at the nest reach the highest values. The model allows the implementation of rainfall events; the water level of the cells raises by the amount of daily rainfall. Fig (9) shows the rainfall pattern, as is divided into three stages. The first reversal occurs between days 35 and 38 after the first egg was laid with 2 cm of rain each day. It is followed by a period of 3 days when

drying occurs, then another mild rainfall event for two days (day 43 and 44) with a three day drying period. Finally, a heavy rainfall occurs for the next 3 days with a total rainfall of 13.5 cm. Figures 10 and 11 show the accumulated food levels for the stork and heron nestlings respectively. We see that almost half of the stork nestlings failed to fledge successfully, whereas herons were able to raise almost two fledglings per nest.

As figures 12 and 13 show, the response of the birds to the early reversals is not as severe as to the last and more drastic (water levels have risen by 28 cm since day 34). That last reversal coincides with the period of the high energetic demands of the nestlings. After the last reversal the birds must spend an increasing amount of time searching, so their time for foraging is less. Pronounced depletion of prey base during that stage occurs and with rainfall increasing the likelihood of a chosen cell to be unprofitable, add up to a decrease in foraging success rates. (Fig. 13). Although foraging rates start increasing after the reversal, it takes about 40-45 days to reach levels 20% lower than the pre-reversal, and since the model assumes a steady and adequate supply of food for successful fledging, it leads to poor reproductive performance. Looking at figure 14 we can attribute the poor reproductive success of storks to the tendency to form flocks. As it is shown almost 80% of the

birds foraging in flocks failed to raise a single fledgling; the only succesful ones were the solitary. Figure 15. shows that foraging in flocks is not beneficial for herons either. All of the solitary herons were successful.

E. UNCERTAINTY/SENSITIVITY TO PARAMETER VALUES

In an effort to assess the role of the sensitivity of the parameters used in both models as relates to model output I varied the parameters for the two models. Parameters from Table 1 were allowed to small (up to 2%) variations and the variance in the output was measured (Table 2). The output variable was total number of successful fledglings. For each parameter a total of 100 simulations were performed using Latin hypercube sampling. For parameters where uncertainty was of concern, a range of possible values was given and simulations were performed under two scenarios (Fig.16) with parameter values from a uniform distribution with the same range.

For both models almost the total (>80%) of the variance in total number of successful fledgings observed was due to four parameters: total food required for fledging, maximum food brought back to nest, daily food requirement, and starvation threshold for fledging. More specifically, for the Wood Stork model the threshold to reach fledging was most important (34%). In the Heron model it was of high importance too (29%)

with maximum food brought back also important (26%). It is quite interesting however that with a high starvation threshold the colony success increases. This happens because of rapid brood reduction and the decreased competition in the nest for resources. So if the (usually youngest) nestling starves and perishes, the nest has a >90% probability as the simulations suggest, to rear both surviving nestlings. Since the analysis serves the purpose of identifying critical parameters as they relate to model predictions it is of concern the finding that almost all of the critical parameters were based on estimates and calibrated values, rather than on accurate data. In this sense, I think, one of the main benefits of modeling, namely exposing areas where data is missing, is demonstrated. Predictive power of the models will improve with the accuracy in estimating parameters.

F. DISCUSSION

The Wood Stork, as our simulations confirm, is the species most sensitive to variations in water level, because unlike visually hunting species of herons, the stork feeds exclusively by non-visual, tactile methods and its feeding efficiency is directly related to fish density. Initiation and success of wood stork colonies depend on high densities of fish concentrated in ponds and other catchment basins during the dry season. The fish on which the wood storks feed

increase in density during the dry season as water levels fall.

Great Blue Herons, on the other hand, appear not to be so dependent on concentrated food supplies (they are affected less by prey dilution) because being visual feeders they can meet their energetic requirements selecting for few but large prey items. Although they were also affected by the rainfall it was to a lower degree. Their colony maintained stable population size.

Both species require approximately 4 months to fledge young and colonies formed late have insufficient time for development prior to the onset of the rainy season which raises water levels and causes desertion.

In simulations where resources fluctuated rapidly with time, resource predictability decreased, and the foraging birds tended to form groups, in an effort to minimize searching time. If temporal heterogeneity is relatively low as in (1), then knowledge of the location of profitable feeding sites (assuming an exponential memory decrease) tends to be important irrelevant to the feeding mode of the species.

The pattern of food utilization and availability in the Everglades suggests why drying patterns might be important in relation to nesting success. Fish must be available in high densities in the central slough area over several months.

This necessitates continual concentration along drying edges and, ultimately, concentration in residual pools. Such a process may require a drying rate sufficient to maintain a wave of concentrated fish over a relatively long period of time. High water level conditions, whether caused by short term rainfall or, alternatively by increased overland flow due to surface-water discharge, reduce fish density by dispersing concentrated fish and, as a consequence, have a pronounced effect particularly in feeding efficiency of Wood Storks.

The maintenance of spatial heterogeneity is particularly of paramount importance concerning top consumer populations, like the wading birds. During the normal dry season and due to the variability of the rainfall pattern the likelihood of a localized large rainfall event, known as a reversal is quite high. Such a reversal in a spatially homogeneous terrain would put nesting colonies of wading birds to an elevated risk. It is the nonuniform spatial distribution (in elevation and vegetation types) that provide a fraction of resourceful feeding areas for the nesting birds, even when such disturbances occur.

Although there is general consensus that altered flow volume and hydroperiods are largely responsible for the long-term decline of wading bird populations, the detailed mechanisms by which this has occured are not well understood. Walters et al. (1990), Hoffman et al. (1993) review various hypotheses. One

of the possible reasons for the severity of the reversals in the altered system is the diking of the majority of the Everglades. In the historic, undiked system, a dry season reversal would have caused reflooding of recently dried peripheral areas, followed almost immediately by recession, quickly regenerating transitional water conditions. Currently, if a reversal raises water levels from levee to levee, transitional conditions cannot be generated in that area until water levels drop back at the base of the levee.

There is a broad agreement that restoration of natural volumes and cycles of water flow through the Everglades will help to reverse the declines in wading bird populations. Short-hydroperiod freshwater marshes may recover relatively rapidly following such restoration efforts. Longer recovery times will probably be required for the long-hydroperiod marshes in the east Everglades, which have been relatively dry for many years and have undergone alterations in soil composition. Bird populations will require some years to increase to historical levels even if restoration efforts are successful, due to possible time lags in re-establishing breeding colonies and the time required for subsequent population growth.

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APPENDIX

Figure Captions

Figure 1. Water depth at the P36 gauge in Shark River Slough of Everglades National Park. Depth is shown by 22 year mean. (Modified from Bancroft et al., 1990)

.Figure 2 Schematic representation of the landscape around a traditional wading bird colony located in the estuarine headwater region of the Southern Everglades: a long hydroperiod marsh surrounded by short hydroperiod peripheral wetlands.

Figure 3. Scenario 1: The number of nestlings in each colony during the entire breeding season.

Figure 4. Scenario 1: The number of fledglings in each colony during the breeding season.

Figure 5 Scenario 1: Distribution of accumulated food intake of the wood stork nestlings at the time of fledging.

Figure 6 Scenario 1: Distribution of accumulated food intake of the Great Blue Heron nestlings at the time of fledging.

Figure 7. Scenario 1: Average fraction of time each bird has been foraging.

Figure 8. Scenario 1: Daily foraging rate (average over all adults). Vertical units: grams of fish obtained per 15 minutes foraged.

Figure 9.Scenario 2: Daily rainfall and water level change between day 30 and 55.

Figure 10.Scenario 2:Distribution of accumulated food intake of the wood stork nestlings at the time of fledging.

Figure 11.Scenario 2:Distribution of accumulated food intake of the Great Blue Heron nestlings at the time of fledging.

Figure 12.Scenario 2: Average fraction of time each bird has been foraging.

Figure 13.Scenario 2: Daily foraging rate (average over all adults). Vertical units: grams of fish obtained per 15 minutes foraged.

Figure 14.Scenario 2: Wood Stork foraging modes as related to colony success

Figure 15.Scenario 2: Great Blue Heron foraging modes as related to colony success

Fig. 16 Results of uncertainty analysis. In all cases variations of the parameter "minimum food for fledging" could account for more than 28% of the total variance.

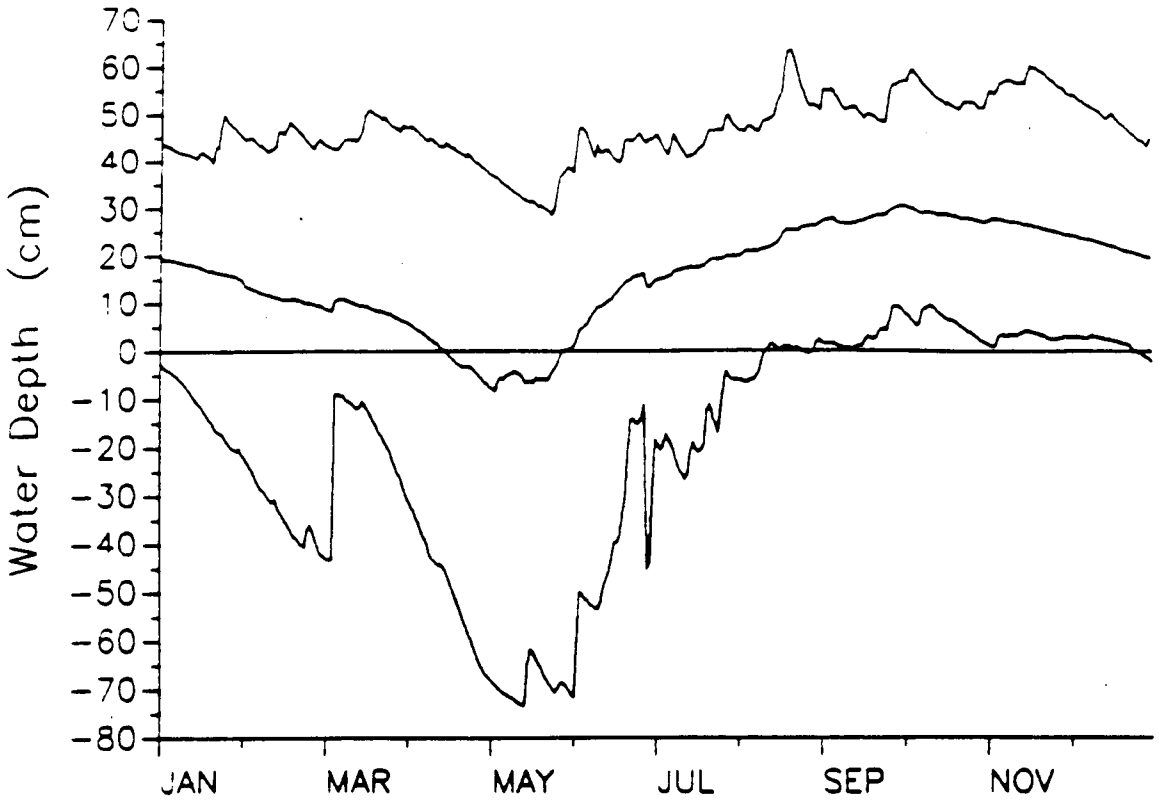

Water Depth (cm)
70
60
50
40
30
20
10
0
-10
-20
-30
-40
-50
-60
-70
-80
JAN
MAR
MAY
JUL
SEP
NOV

Figure 1

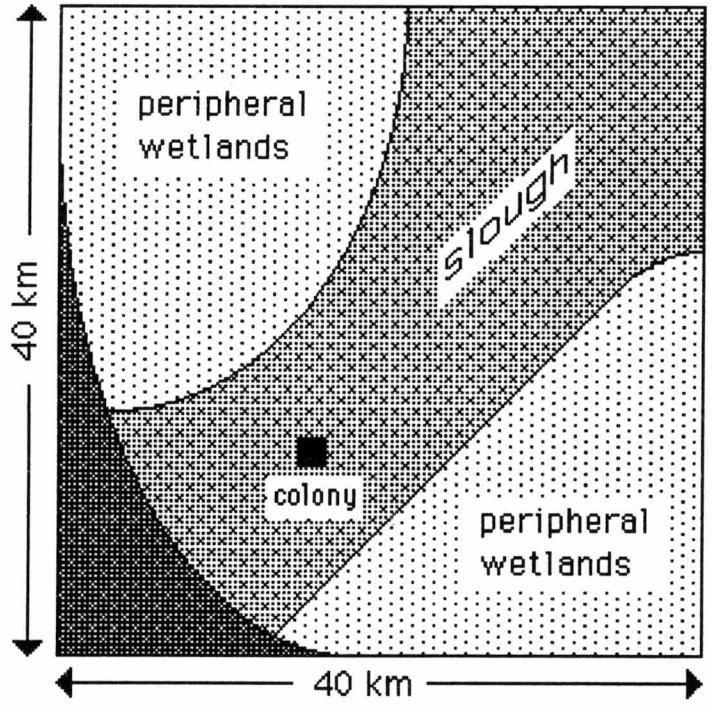
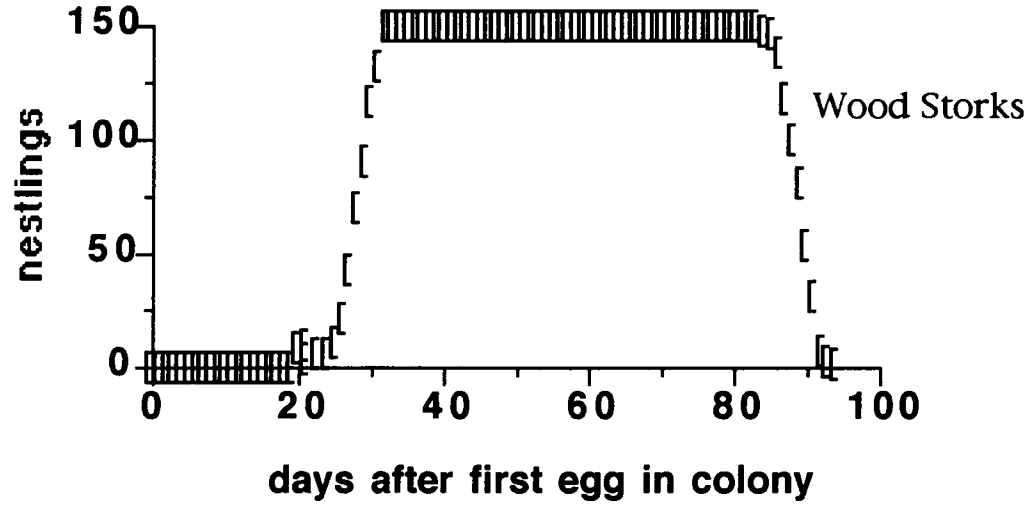


Fig.2 A schematic representation of the landscape around the colony.


150
100
50
0
nestlings
0
20
40
60
80
100
days after first egg in colony
Wood Storks

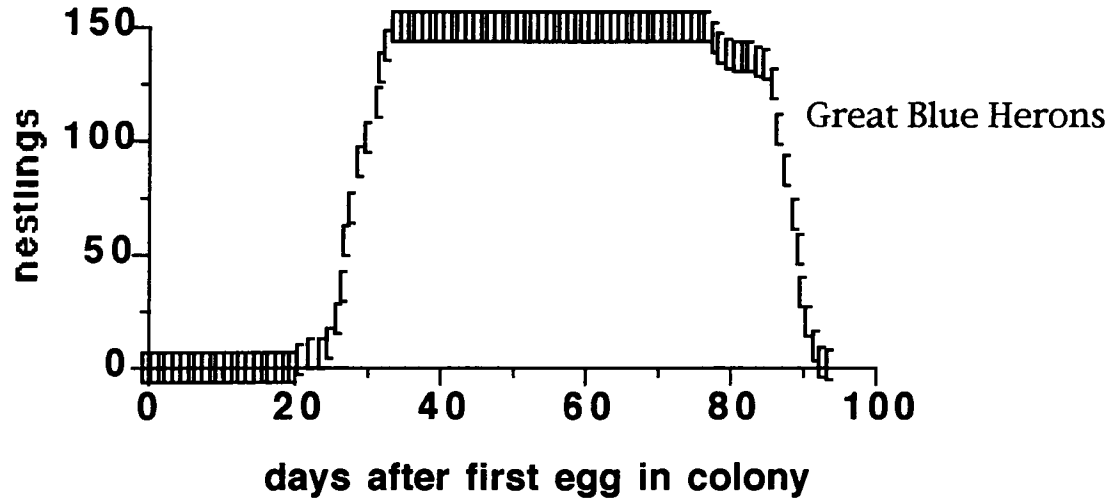

150
100
50
0
nestlings
0
20
40
60
80
100
days after first egg in colony
Great Blue Herons

Fig 3

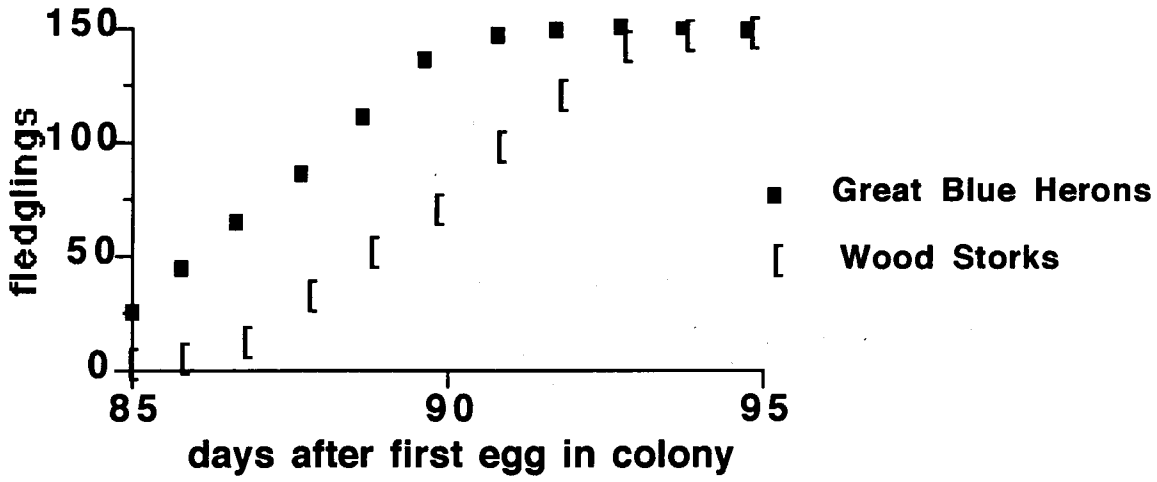

150
100
50
0
fledglings
85
90
95
days after first egg in colony
Great Blue Herons
Wood Storks

Fig 4

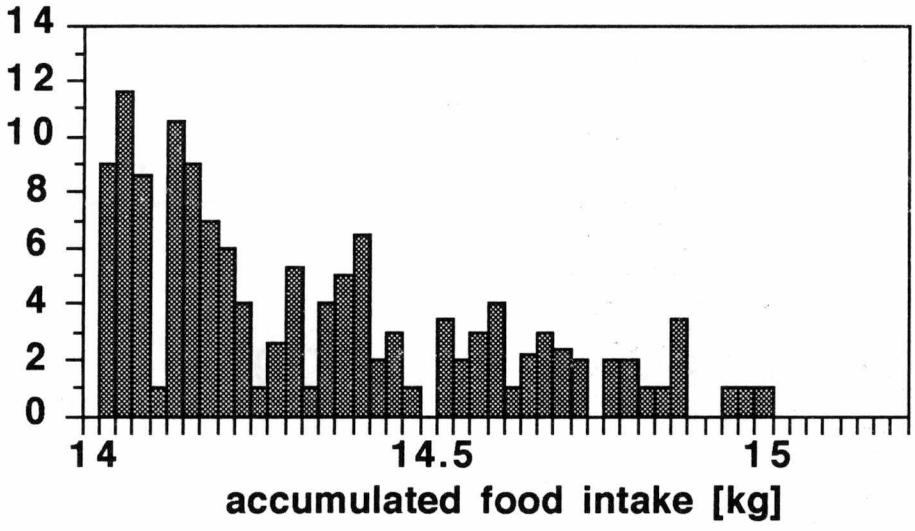


Fig.5

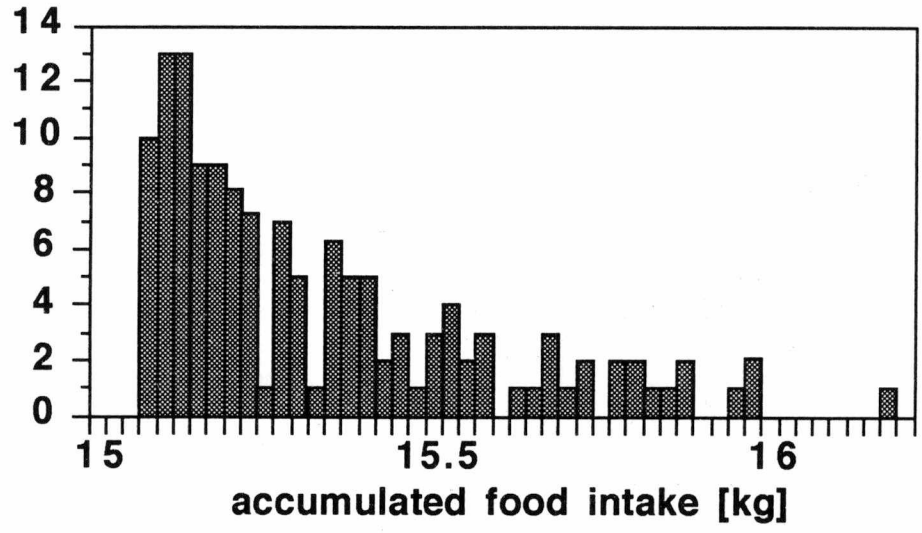


Fig. 6

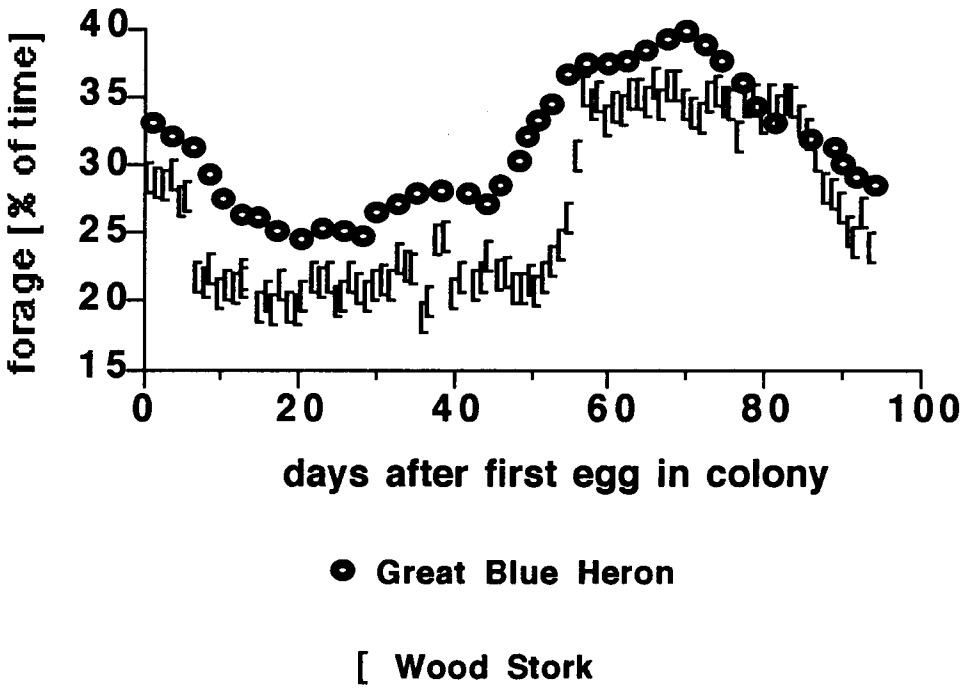

forage [% of time]
40
35
30
25
20
15
0
20
40
60
80
100
days after first egg in colony
Great Blue Heron
[Wood Stork

Fig. 7

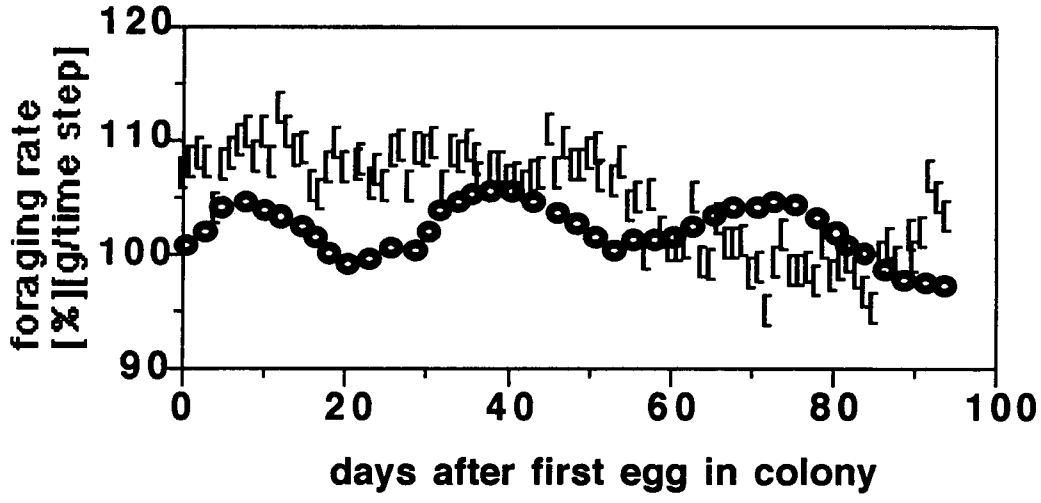

120
110
100
90
foraging rate
[%][g/time step]
0
20
40
60
80
100
days after first egg in colony

Fig.8

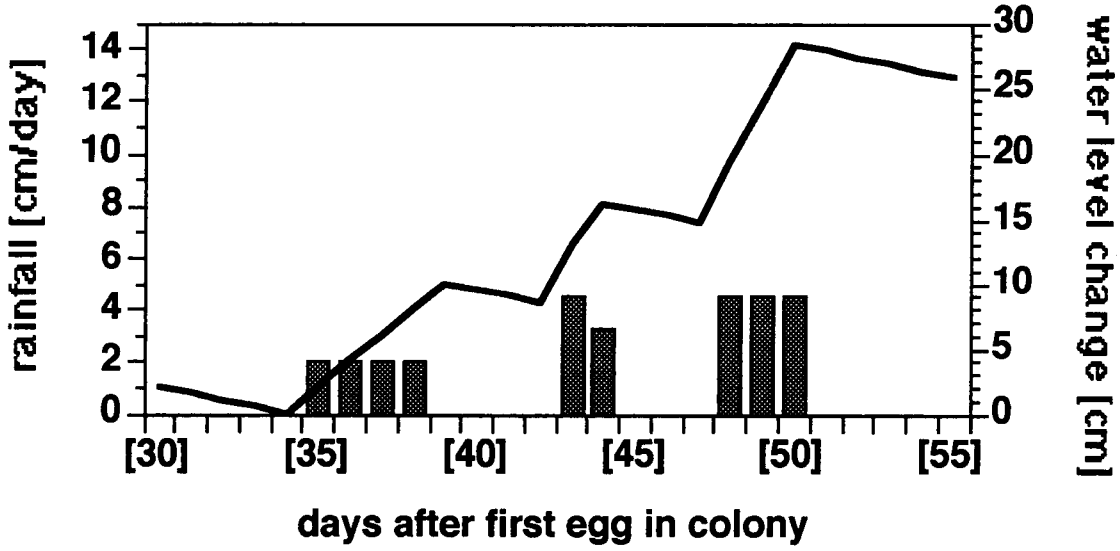

rainfall [cm/day]
14
12
10
8
6
4
2
0
30
25
20
15
10
5
0
water level change [cm]
[30]
[35]
[40]
[45]
[50]
[55]
days after first egg in colony

Fig. 9

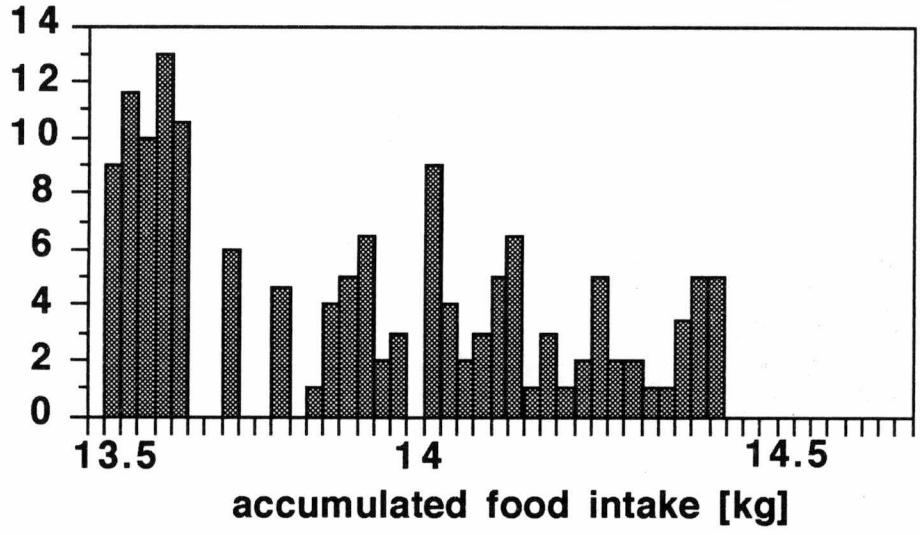


Fig 10

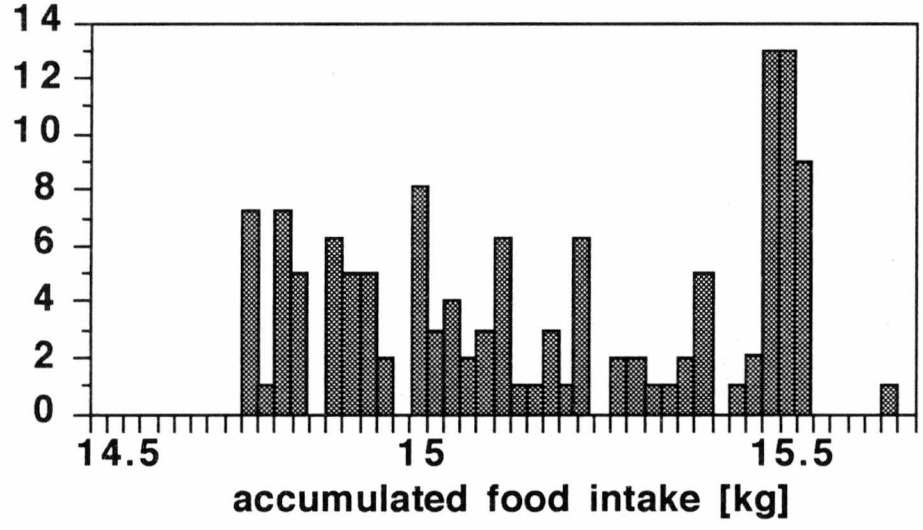


Fig. 11

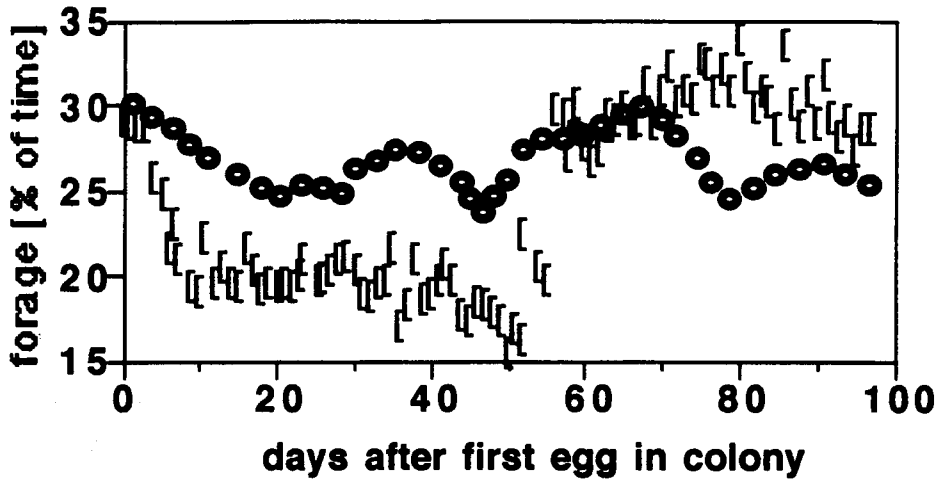

forage [% of time]
35
30
25
20
15
0
20
40
60
80
100
days after first egg in colony

Fig. 12

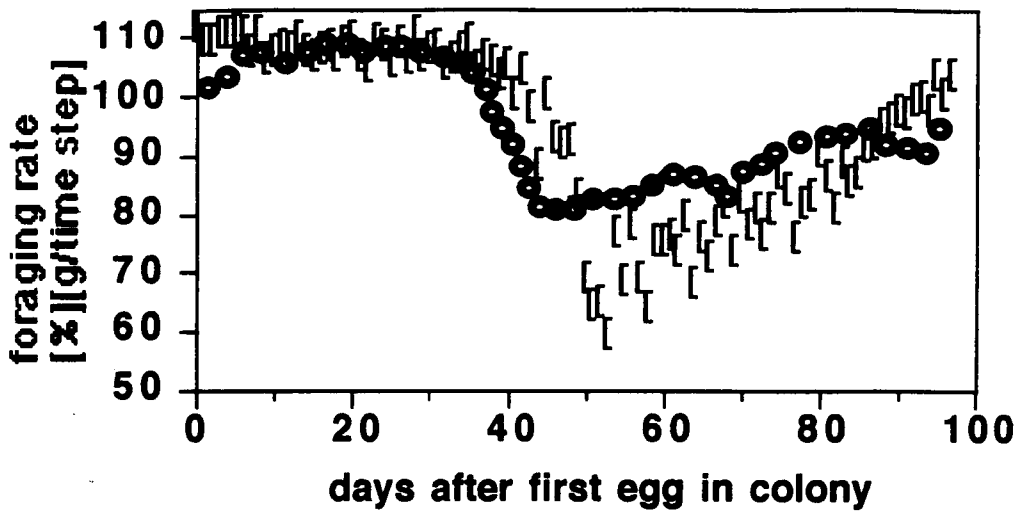

foraging rate
[%][g/time step]
110
100
90
80
70
60
50
0
20
40
60
80
100
days after first egg in colony

Fig. 13

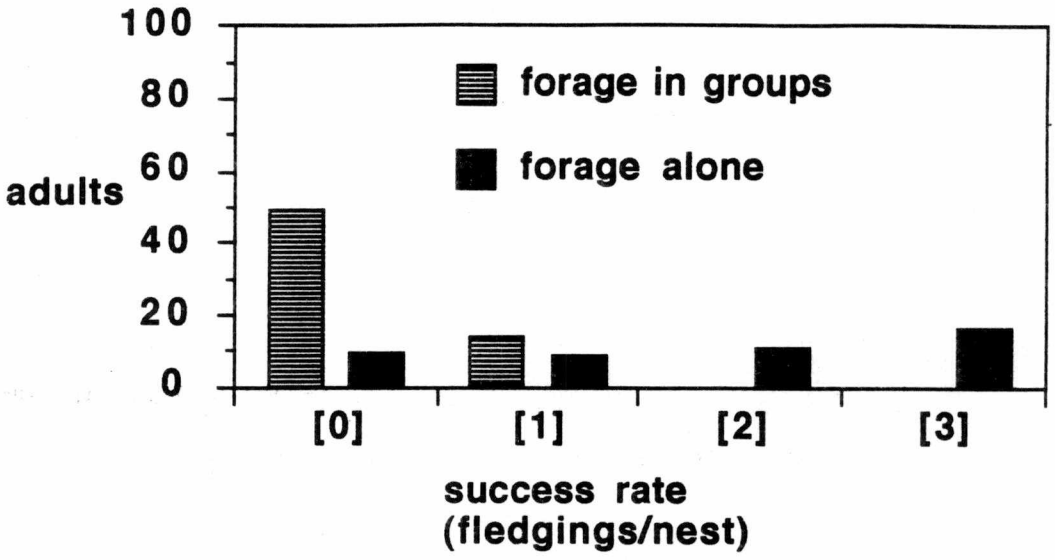

100
80
60
40
20
0
adults
forage in groups
forage alone
[0]
[1]
[2]
[3]
success rate
(fledgings/nest)

Fig. 14

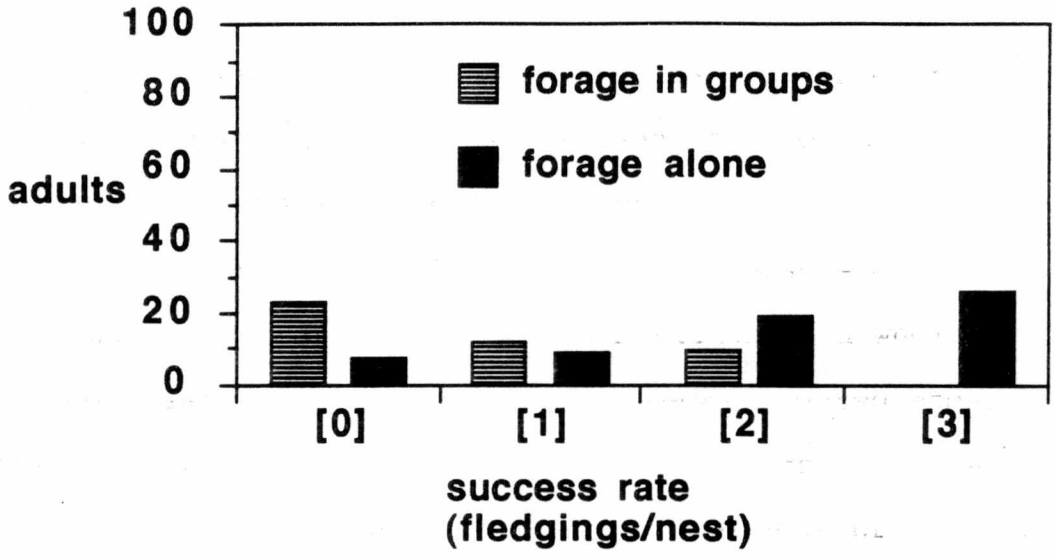

100
80
60
40
20
0
adults
forage in groups
forage alone
[0]
[1]
[2]
[3]
success rate
(fledgings/nest)

Fig. 15

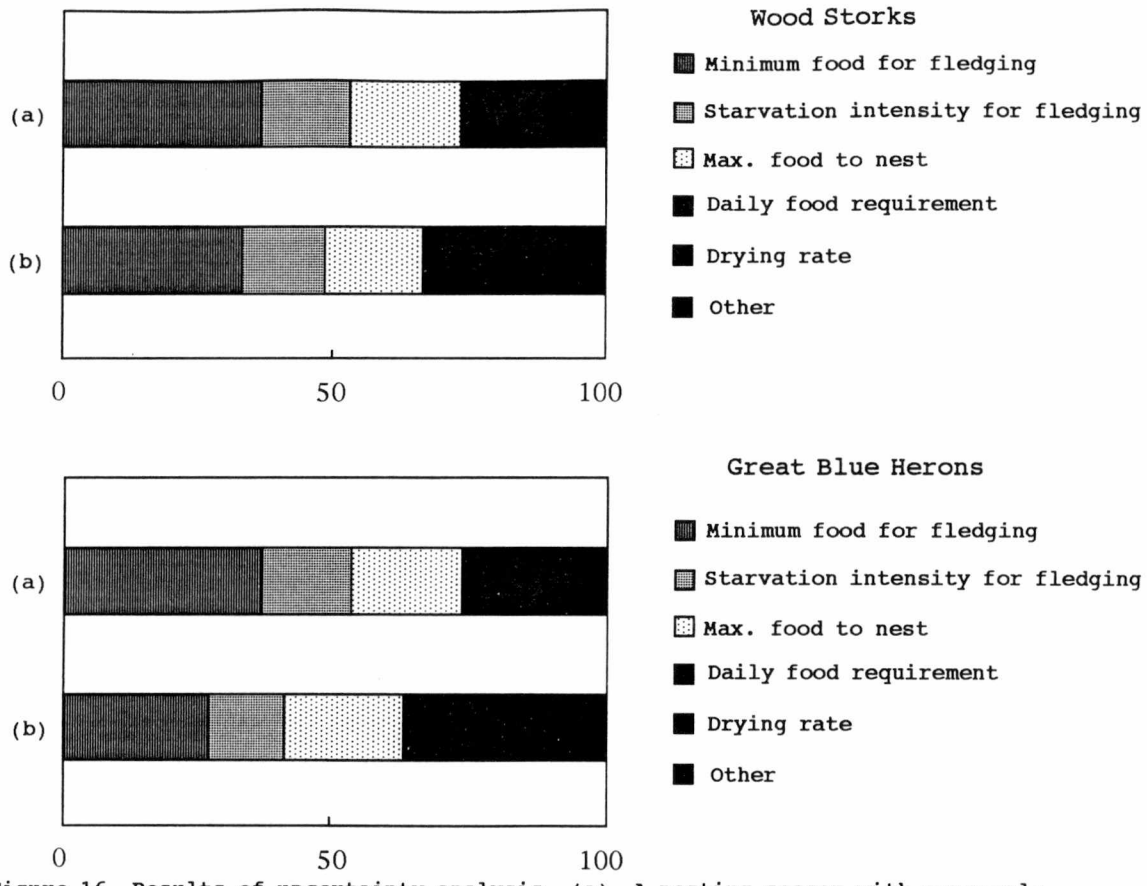


Figure 16. Results of uncertainty analysis. (a) A nesting season with reversals (b) A normal nesting season

Table 1. Table of parameters

Parameter	Wood Stork	Great Blue Heron	References
Weight (kg)	2-3	3-3.5	Palmer (1962)
Basal metabolism (Kcal/day)	147	160	Kahl (1964)
Free flying metabolism	450	510	Kahl (1964) est.
Assimilation efficiency	79%	75%	Kahl, 1964
Maximum distance (km)	15	8	Estimated
Nest initiation threshold (kcal/week)	545	600	Estimated
Number of eggs	3	3	Kushlan, 1978, Palmer 1962
Incubation period (days)	30	28	Palmer (1962)
Total food for fledging (kg)	14	15	Kahl, 1964, Kushlan, 1978
Maximum food in cell (kg)	30	5	Estimated
Days before young leave colony	65	60	Coulter, 1989
Daily food requirement (gr)	500	600	Kahl, 1964
Maximum food to nest (gr)	300	320	Coulter (pers. comm.)
Effective flying speed (km/h)	25	22	Coulter, 1989, Simpson, 1980
Maximum depth for foraging (cm)	40	44	Kushlan, 1978, Palmer, 1962
Probability of solitary foraging	0.5	0.7	Krebs, 1974, estim.
Drying rate (cm/day)	0.50	0.50	Estimated
Fledging feeding efficiency	75%	linear with age	Estimated
Giving up time	15	$\frac{t}{T}$	Estimated

Table 2. Parameters used in sensitivity and uncertainty analysis

Parameter	Wood Stork	Great Blue Heron
Weight (kg)	[2-3]	[3-3.5]
Basal metabolism (Kcal/day)	147	160
Free flying metabolism	450	510
Assimilation efficiency	79%	75%
Maximum distance (km)	[10-20]	[5-15]
Nest initiation threshold (kcal/week)	[520-550]	550-650]
Number of eggs	3	3
Incubation period (days)	30	28
Total food for fledging (kg)	[13.5-14.5]	[14.5-15.5]
Maximum food in cell (kg)	[20-30]	[3-15]
Days before young leave colony	65	60
Daily food requirement (gr)	500	600
Maximum food to nest (gr)	[250-350]	[280-350]
Effective flying speed (km/h)	25	22
Maximum depth for foraging (cm)	40	44
Probability of solitary foraging	[0.3-0.7]	[0.3-0.7]
Drying rate (cm/day)	0.50	0.50
Fledging feeding efficiency	75%	linear
Giving up time	15	$\frac{t}{T}$

PART V

USING AN OBJECT-ORIENTED MODEL FOR ECOLOGICAL RISK ASSESSMENT ON A GREAT BLUE HERON COLONY

A. ABSTRACT

The contribution of certain contaminants to reproductive failure in many avian species has been an ongoing concern. I used the individual-oriented approach in an effort to quantify effects of chronic contaminant exposure on individual birds rather than the population as a whole. This was made possible by the use of an object-oriented model, where individual birds are interacting objects, and their actions are implemented by passing to them appropriate messages. Using this modeling approach a breeding colony of Great Blue Herons (*Ardea herodias*) is simulated as an assemblage of interacting individuals whose daily actions (foraging, growth, feeding of the young) are simultaneously followed over short time intervals for a nesting season. Spatial distribution of the contaminants in prey resources is used on a cell by cell basis and their effects on certain behavior characteristics of adult birds (e.g. foraging efficiency, effects on flying efficiency, parental care) are taken into account. Results show that sublethal effects can have a considerable effect on colony success.

B. BIOINDICATORS OF ENVIRONMENTAL CHANGE

Assessing changing conditions within an ecosystem by monitoring (or even identifying) all of its components, processes, functions, is not possible (Peakall, 1992, Peakall and Shugart, 1993). As a result, a small set of components has to be selected to serve as indicators of wider conditions. Biological components chosen for this purpose are called biological indicators or bioindicators. Much of the theoretical basis of bioindication must result from general systems theory (e. c. Von Bertalanffy, 1968, Odum, 1983). That is, if a system is a sum of parts, described by a system of state variables, interacting subject to a set of rules or processes, the condition of the system could be assessed from a smaller set of state variables. The importance of the structure of the system including hierarchy, scales of organization should be taken into account when choosing bioindicators.

Several aspects of the biology of wading birds make them appropriate bioindicators of environmental change. As top predators, their population responses can serve as signals of environmental changes occurring at lower trophic levels. Their mobility and use of man-dominated landscapes result in their exposure to a number of environmental contaminants that can cause toxic effects. Their colonial nesting and the

subsequent limitations in their activity ranges (feeding) makes them appropriate for small scale sentinels of potential stress. As also concluded from Part IV, their dependency on specific physical aspects of aquatic environments like the hydrology (Kushlan, 1986) makes them potential indicators of change in these physical attributes of their habitat.

Finally, the focus on birds as bioindicators can be made on other criteria. Wading birds, and waterfowl more generally, are of high aesthetic and recreational value to humans. This is reflected, for example, in the fact that in order for a site to be listed as a wetland of international importance under the Ramsar Convention that site must be associated with migratory colonial bird populations. (Ramsar, 1988)

A large number of studies on the fate of contaminants have used wading birds as their target species. As top level carnivores, they accumulate a number of persistent contaminants, including metals, organochlorine pesticides, polychlorinated industrial chemicals and radionuclides.

Wildlife toxicology, the study of the effects of environmental contaminants on the reproduction, health and well being of wildlife has traditionally relied on studies performed in the laboratory, primarily focusing on LC_{50}, and LD_{50} tests. Moreover, wildlife toxicity work that represents effects of avian species existing in nature is difficult to

simulate in the laboratory and difficult to interpret in the field. Hazard assessment consists primarily of matching the concentrations of chemicals in the field, taking into the account both their dispersion and their loss of toxicity since the time of their release, with the threshold concentrations of specific organisms responding to the chemicals in a laboratory toxicity test.

C. MODELS IN AVIAN TOXICOLOGY

Short term predictions of responses of populations to toxicants can be made using a Leslie matrix approach (Grant et al. 1983, Samuals and Ladino, 1983). Toxicological data (dose-response) are used in generating the form of the effect of a toxicant on the demographic parameters of the model. Grant et al.(1983) used a demographic model to assess effects of the pesticide 1080 on a population of great horned owls (Bubo virginianus). They assumed that the toxicant acts only on survival, not fecundity, and also that density-dependent control operates via a linear response of birth rates to changes in population density. A similar model was used by Samuals and Ladino (1983) in an effort to predict recoveries of seabird populations from the effects of oil spills. It was parameterized for herring gulls (Larus argentatus), and used different scenarios (only chicks affected, only juveniles, etc.) for age specific mortality.

An equilibrium stochastic model was used to predict the fate of PCBs and mercury in an aquatic food web (Macintosh et al. 1992). Target species included the great blue heron and the mink. The authors chose a steady-state type of approach instead of a dynamic, because they argued that levels of bioaccumulation are only factors of cumulative dose, and so the rate at which final concentrations are reached is not important.

The bioaccumulation of contaminants by free living organisms has traditionally be modeled using slight variations of the deterministic model that follows:

$$\frac{dC_t}{dt} = k_u C_s - k_d C_t \qquad (5.1.1)$$

where $\frac{dC_t}{dt}$ is the rate of change of contaminant concentration in organism, C_s is the concentration in the infinite source, C_t is the concentration in organism at time t, k_u is the uptake rate constant, and k_d is the depuration or elimination rate constant. The dynamics of this simple model lead to a steady state given by:

$$C_e = \frac{k_u C_s}{k_d}$$

where C_e is the final (equilibrium) concentration of the contaminant in the organism. Assuming that the parameters

k_u, k_d , and C_s are constant we can solve equation (5.1.1) to obtain the analytic solution:

$$C_t = C_e\left(1-e^{-k_d t}\right) \qquad (5.1.2)$$

One of the immediate shortcomings of the model is that it predicts that the concentration in the organism (or some organ, or tissue of the organism) increases at a maximal rate at the time of first exposure. The rate of increase then gradually drops before reaching asymptotically zero. The main assumption of the model that the rate of uptake k_u is constant may not be true under field conditions. Several reasons can account for this, including variability in behavior, food availability, or variability in the contaminant levels across spatial scales. A number of models have been used with modifications of the basic parameters to incorporate multiple sources, multiple elimination components, growth and so forth. Nevertheless, the enhanced realism that more complex models provide will always be depending on the assumptions of the simple model, i.e., constant rates, time or age independence in transition among compartments.

Concerned with the inadequacy of the previous model to take into account time lags occuring in early contaminant rates, Brisbin et al. (1990) used the Richards (1959) equation:

$$C_t = \left[C_e^{(1-m)} - \left(C_e^{(1-m)} - C_0^{(1-m)}\right)e^{\frac{-kt}{}(m+1)}\right]^{\frac{1}{1-m}} \qquad (5.2.1)$$

where C_0 is the initial concentration, T is the approximate time required to attain 95% of the final asymptote and m is a "shape parameter". Different values of the parameter m can produce a variety of fixed-shape sigmoidal curves. For $m = 0$, the Richards model becomes the monomolecular curve (equation (5.1.2) above, for $m = 0.667$ it becomes the von Bertalanffy, and for $m = 2$ it becomes the logistic model. For $m \rightarrow 1$ it becomes the Gompertz model. In the case $m = 0$ the parameter k_d is transformed according to T according to:

$$T = \frac{2(m+1)\cdot(1-m)}{k_d}$$

The model was used by Brisbin et al. (1990) an effort to assess bioaccumulation of radionuclides on American coots (Fulica americana) exposed particularly to gamma-emitter radiocesium ^{137}Cs. The model (equation 5.2.1) with whole body burden C_e of 4.73 Bq/g and a value of $m = 1.2$ provided a better estimate of the actual data than the simple model (equation 5.1.1) Another application involves the bioaccumulation of cadmium by wood ducks (Brisbin et al., 1986b) where the effects of sex and dietary composition are considered using the Richards model (equation 5.2.1)

A Richards type of model, although useful for fitting bioaccumulation data and for providing an empirical assessment of bioaccumulation, does not help us gain insight

into the actual mechanisms responsible for the observed patterns of bioaccumulation.

D. INDIVIDUAL-ORIENTED MODELS IN RISK ASSESSMENT

Ecological risk assessment (Suter, 1992) provides a quantitative basis for comparing risks to nonhuman biota associated with the adverse effects of environmental hazards. The spatial heterogeneity of the landscape is very important in the case of regional risk assessments (Graham et al., 1991). It has been recognized that in order to perform a risk analysis for a particular toxicant one cannot afford to look at all the species in the risk-prone area. The use of bioindicators, as explained above, can help in extrapolating effects of toxicants in a biological community.

Great Blue Herons (*Ardea herodias*) occupy the top consumer position in the food webs of many river and lake communities (Fig 1), and as such they can serve as bioindicators of environmental health.

In my study I focus on a population of Great Blue Herons that occupy a colony in Poplar Creek, Tennessee, with considerable microhabitat heterogeneity being exposed to contamination by PCBs. A proper modeling approach should incorporate both spatial heterogeneity and life histories of the birds, focusing in detail on the processes by which the organism is

exposed to the contaminant and by which the contaminant can affect the organism.

The individual-based approach was chosen because of the difficulty of state-variable models in dealing with local interactions among individuals and the effects of spatial variability. In the cases of spatially heterogeneous environments, aggregating populations based on total numbers (i.e. traditional state based models) or physiological attributes (size, age) does not offer sufficient detail to adequately reflect the spatial variability encountered by the population.

Individual-oriented modeling, or *i*-state configuration modeling (Caswell et al., 1992), offers a unique tool to incorporate a high degree of realism by simulating simultaneously biological phenomena at the individual level such as foraging, movements through space, local interactions with conspecifics and so forth (Wolff, 1994).

With the individual-oriented approach the variation in physiological characteristics (e.g. size, weight, age, fitness) within a local population can be taken into account since each individual has its own set of characteristics that are updated by the simulation (Fig.1). In this manner I avoid the common problem of following the "average" individual of state variable models. It is quite often the

case that such an average individual not only does not exist, but gives a poor representation of a population characterized by variability, since, especially in stressed populations, atypical individuals succeed determining the recruitment of the whole population. This approach also offers the tool to incorporate short term variability in the model, since the time step used is quite small (days or less) as compared to the ones used in state variable models.

However, a common problem with constructing such a model is the large number of parameters and data needed. Usually data are aggregated to spatial scales that are too coarse to support the needs of a spatially explicit model.

E. MODEL COMPONENTS

A first version of the model was constructed for Wood Storks, taking into account the effects of different water level patterns on their reproductive success. (Wolff,1994)

The Great Blue Heron model consists primarily of the following submodels:

(i) an explicit landscape submodel surrounding the colony,

(ii) a resource environment for the birds, containing prey information,

(iii) a contamination profile of the landscape,

(iv) behavioral submodels for the adult birds, and their nestlings including their physiology and energetics,

(v) bioaccumulation submodel for the uptake of the contaminant.

A synoptic description of the basic elements of the model follows. The landscape submodel provides a dynamic representation of a 10 by 10 km area surrounding the colony (fig. 3) subdivided to 25,600 square cells (with a side of 62.5m each) with information of elevation and water depths of each cell. Effects of rainfall to the water level are also taken into consideration.

The resource environment submodel keeps track of the availability of fish in each cell that is inundated. The main areas used for foraging consist of the shorelines of Clinch River, Poplar Creek, and Watts Bar Lake (Fig. 3) Herons can form flocks on profitable cells, thus reducing (or even depleting) the local resources. The model in its current version does not allow dispersion of fish from one cell to another; empty cells however can be replenished after a short period (2-3 days).

The contamination profile assigns PCB concentrations on each cell of the resource environment, based on sampled

concentrations in fish at different locations within the landscape. A major source of uncertainty enters the model at this stage since it is not feasible to have accurate estimates for all (25,600) of the cells. Statistical methods, however are used to deduce the local concentrations. The situation is easier dealing with point sources of contaminants (e.g. in a river) where I could simulate contamination levels as a gradient.

Behavioral rules

The rules governing the behavior of adult and nestling herons have been described in detail earlier (Part IV). Summarizing, each bird's behavior is controlled by more than 200 behavioral rules. There are both probabilistic and deterministic rules determining a variety of processes. There are rules for the way of searching for food, the foraging efficiency of the adults, the feeding of the nestlings, the energetics based upon food consumption of both the adults and the nestlings, ways adults interact with their mate (during nest attendance, incubating the eggs) and other conspecifics (when to initiate a nest, how to join a flock, etc.) (Fig.4) The foraging rules do not provide optimal yield; they are instead opportunistic. For example a bird has a knowledge of locally available (as far as water depth) cells before it selects one. However it does not know

whether the chosen cell is also resource profitable, so there is possibility for mistakes.

Foraging behavior

Great Blue Herons, like most piscivorous wading bird species, can forage only in shallow water areas with a water depth range of 10-40 cm. They are visual feeders (Kushlan,1978) and can take a variety of prey items within a wide size range (Palmer, 1962). The model assumes a uniform prey base consisting of the species Gizzard Shad (Dorosoma cepedianum) based on abundance (>70%) in the herons diet in the simulated colony (TVA, 1985).

The success or failure of the colony depends on the ability of the adult birds to forage successfully and bring adequate food back to their nestlings during the critical period after the hatching of the eggs and before fledging The model assumes that if a nestling does not receive enough food (for herons an estimate of 14 kg throughout the nesting season is given) during regular intervals does not fledge successfully.

F. BIOACCUMULATION MODEL

Exposure submodel

In the bioaccumulation model described below the basic model (eq 5.1.1) was modified to be used in an spatially explicit simulation model. First, the resource environment had to

serve as the basis of bioaccumulation. The foraging areas that Great Blue Herons could utilize were mainly the shorelines of Clinch river, and Poplar Creek around K-25 plant, along with Watts Bar Lake (fig. 6). Based on data of PCBs on local fish populations (TVA, 1985), first the resource environment is assigned PCB bioconcentration values. So in each cell (that contains fish) a bioconcentration value is given. The data show a gradient in PCB values along Clinch River and Poplar Creek with a point source at K-25 plant. Figure 6 shows that the highest concentrations were sampled in Mitchell's Branch (0.8 ppm), and the lowest east on Poplar Creek (0.12 ppm).

I modified the simple model in equation (5.1.1) for the bioaccumulation of PCBs on the herons as follows:

Each bird has its own instance variable (daily_PCB_intake) calculated as the total burden (mg) of PCBs taken from food on a daily basis. This is calculated as follows:

$$itsdaily\_PCB\_uptake(mg) = \sum_{i:all.foragingcells} fish\_eaten\_atcell[i](g) \cdot amountofPCBs\_atcell[i](\frac{mg}{g})$$

(eq. 5.3.1)

Then I calculate the bioaccumulation levels based on the following reasoning:

Assume again the simple model

$$\frac{dC_t}{dt} = k_u C_s - k_d C_t$$

Because there is spatial variability, C_s cannot be assumed to be constant. The product $k_u C_s$ (uptake rate) depends on the foraging history of each bird. Substituting F(t) for the uptake (mg) from fish and if w (kg) is the weight of the individual bird then $C_s(t) = \frac{F(t)}{w}$ is the concentration (ppm) of PCB on the bird. Therefore equation (5.1) becomes:

$$\frac{dC_t}{dt} = k_u \frac{F(t)}{w} - k_d C_t \qquad (5.3.2)$$

a first-order nonhomogeneous equation that yields the solution:

$$C(t) = \frac{k_e \cdot e^{-k_d t}}{w} \int_0^t e^{k_d s} F(s) ds$$

Since the model updates bioaccumulation on individuals on a daily time step I calculated the daily bioaccumulation as it changes from day t to the next $t+1$ as follows:

$$C(t+1) = \frac{k_e \cdot e^{-k_d (t+1)}}{w} \cdot \int_0^{t+1} e^{k_d s} F(s) ds =$$

$$= \frac{k_e \cdot e^{-k_d (t+1)}}{w} \cdot \int_0^t e^{k_d s} F(s) ds + \frac{k_e \cdot e^{-k_d (t+1)}}{w} \cdot \int_t^{t+1} e^{k_d s} F(s) ds$$

Since $F(t)$ is calculated from (5.3.1) for the particular day $t+1$ we can consider it as a constant (for integration purposes)

Thus we have:

$$e^{-k_d}\frac{k_e \cdot e^{-k_d t}}{w}\cdot\int_0^t e^{k_d(s-t)}F(s)ds+\frac{k_e}{w}F_{T+1}(1-e^{-k_d})=$$
$$e^{-k_d}C(t)+\frac{k_e}{w}F_{T+1}(1-e^{-k_d})$$

Therefore the accumulation is updated daily with the use of the instance variable *itsPCBioaccumulation* keeping track of the total PCBs in the organism.

$$itsPCBioaccumulation = e^{-k_d} itsPCBioaccumulation + \frac{k_e}{w}(1-e^{-k_d}) itsdaily\_PCB\_uptake$$

Female birds are also assumed to shed PCBs by egg-laying. I assumed a .012% of their PCB burden to be passed on each egg they laid.

Effects submodel

The next task of a bioaccumulation model is to be able to predict effects of the contaminant on the birds. There are a number of different ways a contaminant can harm an avian population. The most acute effect would be death. Based on simulation results, that was not possible according to local daily uptake rates (<1 ppm) and lethal concentration values (>170 ppm). However, sublethal indirect effects are also common, including effects on egg quality, clutch size, malformations in embryos, and behavioral effects on parents during the breeding cycle (Fig.5). Pigeons receiving repeated doses of methylmercury showed a disorderly pattern

of motor responses, until eventually, gross motor impairment in locomotion was observed and responding ceased (Norton, 1980). In a study of Caspian Terns reproduction in the Great Lakes (Mora et al., 1993) reproduction was negatively correlated with the mean concentrations of PCBs in the plasma of the breeding adults. Ohlendorf et al. (1978) documented eggshell thinning in the black-crowned night heron as effect of pollutants.

Without having the intention to understate the importance of effects on eggs and hatching success, the present study focused on effects on the efficiency of the parent birds to forage and feed their nestlings. Without having quantitative information a number of assumptions were made regarding the ways the foraging and the flying efficiency could be impaired using linear dose-response forms as shown on figures 10 and 14. Table 1 lists the parameters used and their values.

G. SIMULATION RESULTS

I ran simulations (100 runs for each case presented) following a small colony of Great Blue Herons (50 pairs) at the location of interest (in Poplar Creek, adjacent to K-25 plant). Data were not available to allow simulating real situations in full detail. However, to illustrate the potential of the modelfor incorporating detail into account I used some relaxing assumptions whenever the data was scarce.

That data scarcity was more pronounced in fish abundance data and contaminant levels on a cell to cell basis, since those were not provided in such a resolution.

In the first simulation results presented I used a variable contamination profile with PCB concentrations in fish extrapolated from collected data on PCBs (TVA, 1985) on resident fish populations (Fig. 6) and I was interested mainly in the PCB levels in adult birds after a breeding season. I wanted to focus on the PCB levels for this period since raising of the young requires heavy feeding, and if that occurs in a contaminated area it would result in elevated bioaccumulation. First I describe results on simulations where no behavioral effects are implemented. The reason for this is to compare bioaccumulation of PCBs to lethal levels or levels that were considered to cause severe effects.

The total PCB dietary ingestion criterion for protection of birds has been proposed as 3 ppm (Eisler, 1986). That was the suggestion from an experiment on screech owls (Otus asio) that was fed 3 ppm PCBs (Aroclor 1248) for two breeding seasons without exhibiting effects on reproduction (number of eggs per clutch, hatching success, embryo malformations, and shell thickness).

In the following table (Table 2) average PCB concentrations and standard deviations on birds are listed. I ran 100 simulations under each contamination profile; the ranges e.g. 0.03- 0.05 ppm refer to normalized uptake rates from actual data values given at monitoring locations. Since data were available on the bluegill population, the data had to be calibrated (based primarily on the lipid content) to levels on shad, in order to be used in our simulations. Fig. 7 shows the results of simulations where no behavioral effects were implemented.

In the results we see that the given landscape with an estimated fish abundance can support the energetic needs of all adults and their nestlings, so all nestlings fly successfully. Looking at the PCB values on adults we see no evidence of lethal levels (mean = 55.94, s. d. = 33.78). In Table 2 the results show an increase in the average PCB concentration of adults with increasing levels of contamination in fish. The last range of values corresponds to sample fish data (Fig. 6). In Fig. 8 I present sample individual PCB concentrations through time. By looking at the spatial characteristics of contamination another source of variability is introduced. In Fig. 9 we see significant differences in the PCB concentrations comparing adults foraging in "clean" (< 0.3 ppm) and "contaminated" (> 0.8 ppm) locations. We see that the model predictions do not

support the likelihood of death as an effect of PCB contamination, since clearly the values are distant from 170 ppm.(the concentration assuming daily uptake rates of 3 ppm). So only sublethal behavioral effects were modeled.

First, I looked at effects of PCBs on foraging efficiency. Since the foraging strategy of visually feeding birds, like herons, can be affected by physical impairment, like slowness and gradual loss of motor-coordination skills, their foraging efficiency was modified to account for this. A simple linear dose-response curve (form I) was used to implement this effect (Fig.10) The same figure describes also feeding rates of unimpaired adults.

From the results (Fig. 11) we see that a decrease in the foraging efficiency as a result of bioaccumulation can cause a number of unsuccessful nestlings. In this case 23 nestlings were not able to fledge successfully. Varying the threshold of the decrease from 60 ppm to ±10 ppm could produce only 10% variation in the final results (number of successful fledglings). We also see lower overall PCB levels in adult birds (mean = 49.15 ppm, s. d.= 28.59) as compared to the no behavioral effects case (mean = 55.94 ppm, s.d.= 33.78) that is a result of a decreased feeding performance. If the form of the dose-response function would change (Fig. 12) to account for a hyperbolic form of decrease in foraging efficiency we see (Fig. 13) that although the overall

bioaccumulation levels are similar (mean = 56.08, s. d.=33.47), the number of unsuccessful fledglings is reduced to 23. The obvious difference in the two dose-response functions used is the form in the decrease of foraging rate in (II) since it predicts more than 50% decrease in foraging efficiency at the level of ~110 ppm, whereas in (I) that happens at a lower concentration (~90 ppm). So individual adults with high (>90 ppm) concentrations cannot forage as efficiently under (I), and that results in lower food back to the nestlings.

Herons tend to spend time flying from the colony to foraging sites and back (during feeding of young 3-4 trips daily are taken), or within foraging sites. I wanted to investigate what the consequences of an effect on flight efficiency as a response to elevated bioaccumulation would have to the colony success. In the model I used a simple piecewise linear dose-response form (fig.14) to reflect changes in flight efficiency. Herons use an average flying speed of 20 km/h. The effect of PCBs had a linear decrease of 20% in flying speed starting from levels of 50 ppm to 85 ppm and more than 70% until 100 ppm. Since concentrations rarely exceeded 90 ppm, the latter part of the curve did not contribute much to the flying effects. Fig. 15 shows that results for this case. We see that the effect on flying speed resulted in the failure of 16 nestlings. Adult concentration levels were

normal (mean = 61.35, s. d. = 36.54). Next, combined effects on foraging efficiency and flying speed were implemented. I simulated combined effects of foraging form (I) and flying speed. In the simulation results (fig. 16) 41 nestlings received insufficient food for fledging; 10 exceeded total PCB burdens and fail to fledge too. The mean PCB level in adults is 60.75 ppm (s. d.: 34.89). If foraging efficiency is of the form (II) and the flight effect is implemented (Case 6) the reproductive performance is improved (fig. 17): 40 nestlings were below the food threshold for fledging and 2 are over the contamination threshold.

H. EPILOGUE

The role of spatial heterogeneity in the effort to conserve biological populations under stress has been recognized as very important. The use of different modeling techniques is usually suggested in an effort to understand how these populations respond to different restoration scenarios.

Spatially explicit modeling has recently been used in a variety of ecological problems in an effort to quantify patterns and link them to ecological processes and mechanisms (Sklar et al., 1991, Turner et al , Kolasa et al. 1991). It may also be used to estimate the fate and the effects of contaminants in a landscape. This can be accomplished by means of several spatial scales for different ecological

processes and different sources of contamination. Simulation modeling, and in particular object-oriented modeling can serve integrating the above in a unique way. However, the approach is usually limited by the lack of appropriate data. Especially in the field of wildlife toxicology the "appropriateness" of data is a point on which not everyone agrees.

Most field studies show effects of synergism of a variety of toxicants; extrapolating to the the toxicant of interest is not easy. Another problem is the complexity of the models. In many cases it is not clear how much physiology should be considered. For example, in an experimental study on the effects of Dieldrin on Brown-headed Cowbirds (Molothrus ater) it was observed that relatively low levels in their brains (2 ppm) was the cause of cessation of feeding (Heinz and Johnson, 1980). Starvation in turn was the cause of more mobilization of the toxicant from the fat tissue and consequently elevated levels in the brain leading to death. For herons it has been observed (Ohledorf, 1979) that individuals found dead as a result of organochlorine poisoning had unusually low lipid levels (less than 1%) as a result of mobilization of the toxicant from fat. Introducing physiological processes in detail in a model, including effects on different organs, requires data for model parameterization that are very scarce.

In field studies of toxicants on free-living organisms effects on reproduction and survival have been demonstrated, but not feeding behaviors. In the cases where populations have survived the effects of a toxicant it is not clear whether they succeeded by changing foraging behaviors, or even prey diet (Peakall, 1985). So whether the organism has developed some learned aversion to the contaminated food is yet to be explored. Lacking adequate information regarding the above factors, I have not implemented them in the model. The birds cannot distinguish among fish with elevated rates of PCBs. In this study I demonstrated that contaminant-induced changes in avian reproduction have potential ramifications to the overall reproductive success, through sublethal effects. It was shown that changes in parental behavior may be critical for colony success, especially in the case of altricial nestlings, like the herons.

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APPENDIXES

APPENDIX 1: Object-Oriented Modeling

Object-Oriented Modeling (Rumbaugh et al., 1991, Martin et al., 1992) with the attributes of inheritance, polymorphism, data protection and modularity, provides a natural framework for simulating real-world phenomena. The implementation of an *i*-state configuration model consists of a set of objects representing individuals, an object defining the scope of interactions among individuals (interaction structure object), and a set of objects describing the environment.

An individual in our model is a single object whose *i*-state (age, fitness, size, etc.) is fully characterized by the object's data, and the interface between the individual and the rest of the model is provided with the methods (forage, fly, search, etc.) of the object. Individuals are organized into different classes, based on their intrinsic differences.

Classes of objects are created by defining: (i) instance variables pertaining to each individual organism, and (ii) instance methods describing the actions that individual should take based on its current status.

For example, there are attributes shared by all individuals (age, location) in the superclass "individual bird", and attributes like "laying eggs" pertaining only to individuals in the "female" subclass (Fig. 18). The spatial environment is modeled as a set of cell objects, each characterized by abiotic data (elevation, water depth, contamination level) and biotic data (prey resources, current number of adult birds in cell). The cell methods update the status of each cell.

The modeling approach I am presenting has some similarity with the cellular automata approach (Toffoli et al., 1988), since they both deal with entities moving (living in general) in a 2-dimensional grid. However, there is a major conceptual difference regarding the way each individual's daily actions are implemented. Instead of updating each individual every time step, like in a serial simulation, I use the event-driven simulation approach. The system modeled consists of a set of interacting individuals (objects) that can communicate with each other by sending and receiving messages and changing their status in response to those messages. This approach is in accord with the general idea

of natural events being concurrent, i.e. natural events cause other natural events to happen, based on their hierarchical status and their operating scale, rather than all being subject to some uniform clock. This approach offers a competitive advantage regarding computational speed, since objects (individual organisms or spatial units) that have not received or sent any messages regarding their status do not need to be updated by the model for as long as they remain "idle".

APPENDIX 2 Figure captions

Fig. 1. Great Blue Heron in Food Web. Great Blue Heron (Ardea herodias) is one of the top carnivore consumer species in many river and lake ecosystems.

Fig. 2. Map of the colony.

Fig.3 A schematic representation of individual-based models in ecotoxicology. Physiological characteristics a,b,...,g are sampled from their initial distributions and allocated to individuals. $F_i(t)$ represents the status (a vector) of individual i, and R(i) is the individual response. From these we deduce the population response

Fig.4. A state diagram representing the implementation of the "searching flight" rule. Objectives are: (i) find a feeding site, and (ii) calculate flight time.

Fig. 5. Indirect sublethal effects of toxicants on avian reproduction in the case of altricial nestlings.

Fig. 6. Average concentrations of PCBs (μg/g, wet weight) in fish collected in Fall 1989 at sites on the Oak Ridge Reservation (from Oak Ridge Environmental Report, 1990).

Fig.7. Assuming no behavioral effects. Distribution of PCB concentrations in adults and food per nestling. All nestlings fledge successfully.

Fig.8. PCB levels on sample individual birds based on uptake rates of: (a) 0.8 - 1.1 ppm,(b) 0.5 - 0.8 ppm, (c) 0.3 - 0.5 ppm)

Fig 9. Differences in PCB levels in sample individuals resulting from differences in contamination at foraging sites. curve (a) is the concentration of an adult foraging mainly in the Mitchell Branch and K-25 area, (b) is of an adult that used primarily feeding locations in the northeast of the landscape (east on Poplar Creek)

Fig.10 Assuming a reduced foraging efficiency based on a linear dose response function (Form I). Below, functional response of a healthy heron.

Fig. 11. Simulation results for effects on foraging efficiency (Form I). A total of 34 nestlings fail to fledge.

Fig. 12. Form II of effects of bioaccumulation on foraging success.

Fig. 13. Simulation results assuming effects on foraging success (Form II). A total of 23 nestling below energetic threshold, fail to fledge.

Fig 14. Effect on flying speed

Fig 15. Simulation results assuming effects of contaminant on flying: A total of 16 nestlings fails to fledge.

Fig. 16. Simulation results of combined effects on foraging (Form I) and flying. A total of 51 nestlings fails to fledge.

Fig. 17. Simulation results of combined effects on foraging (Form II) and flying. A total of 42 nestlings fails to fledge.

Fig.18 Class hierarchy of individual organisms. The solid lines represent class-subclass relations; the dotted are class associations.

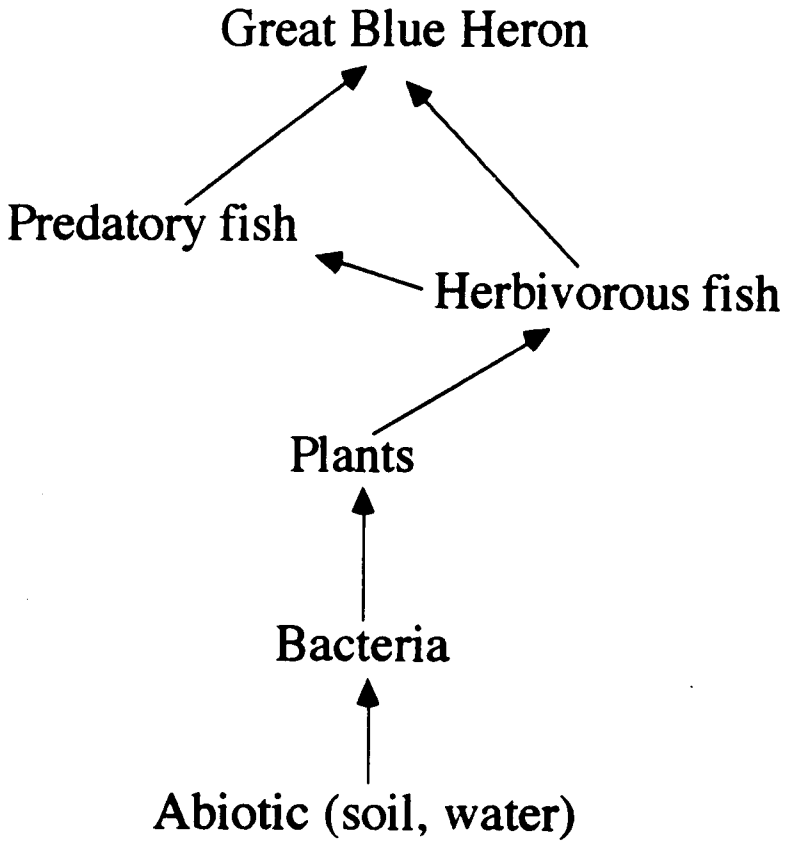

Great Blue Heron
Predatory fish
Herbivorous fish
Plants
Bacteria
Abiotic (soil, water)

Figure 1

Fig. 2. Map of the colony.

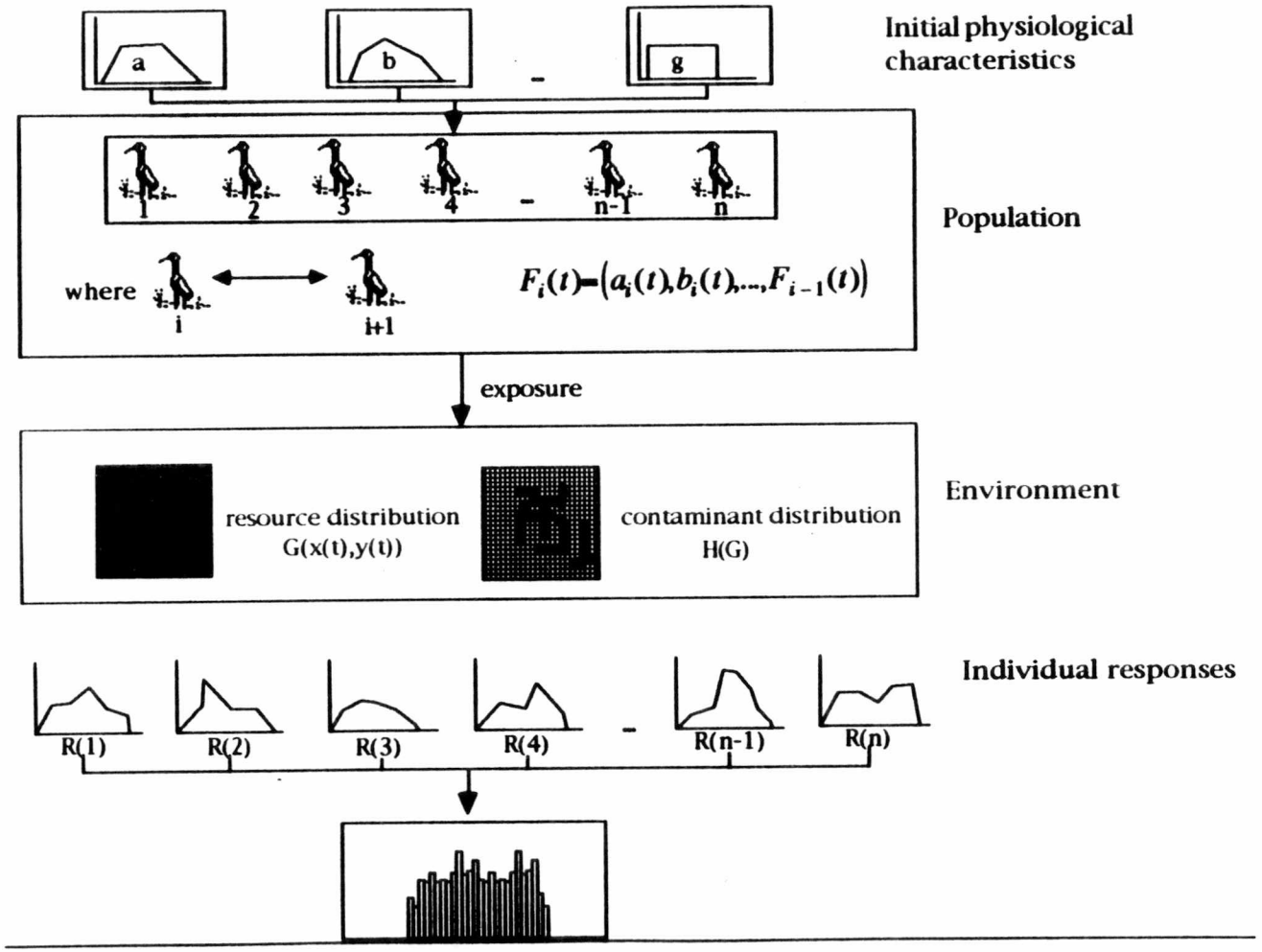

a
b
g
Initial physiological characteristics
1
2
3
4
n-1
n
Population
where
i
i+1
$F_i(t)=(a_i(t),b_i(t),...,F_{i-1}(t))$
exposure
resource distribution
G(x(t),y(t))
contaminant distribution
H(G)
Environment
R(1)
R(2)
R(3)
R(4)
R(n-1)
R(n)
Individual responses

Figure 3

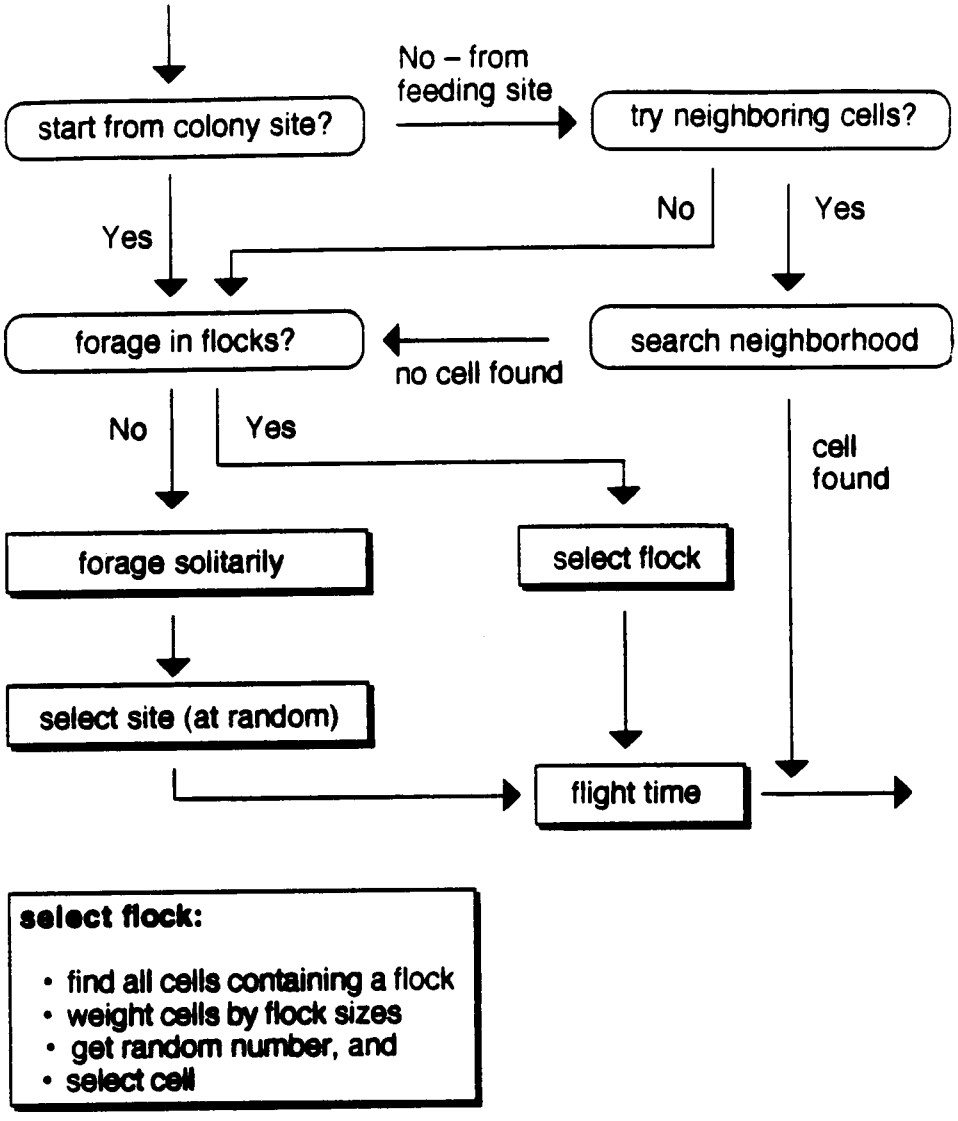

start from colony site?
No – from feeding site
try neighboring cells?
Yes
No
Yes
forage in flocks?
no cell found
search neighborhood
No
Yes
cell found
forage solitarily
select flock
select site (at random)
flight time
select flock:
• find all cells containing a flock
• weight cells by flock sizes
• get random number, and
• select cell

Figure 4

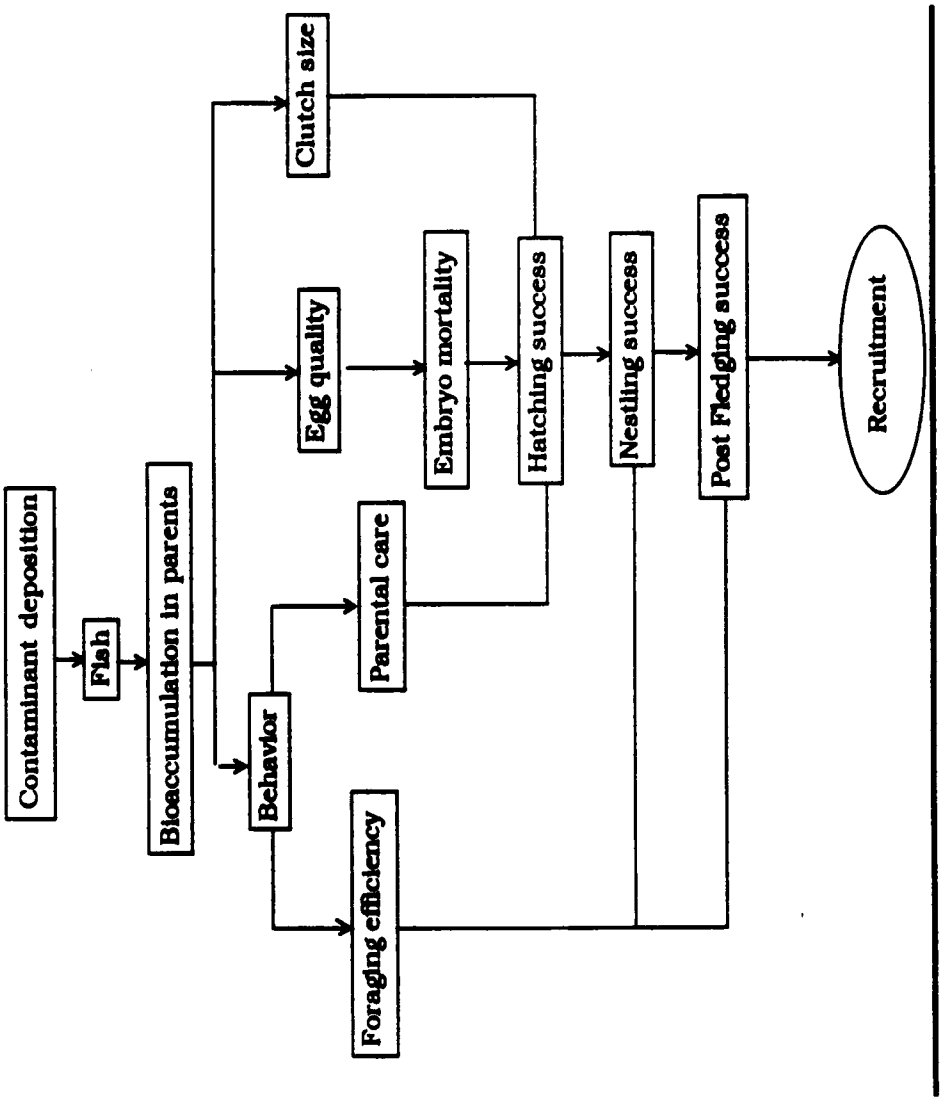

Contaminant deposition
Fish
Bioaccumulation in parents
Behavior
Foraging efficiency
Parental care
Clutch size
Egg quality
Embryo mortality
Hatching success
Nestling success
Post Fledging success
Recruitment

Figure 5

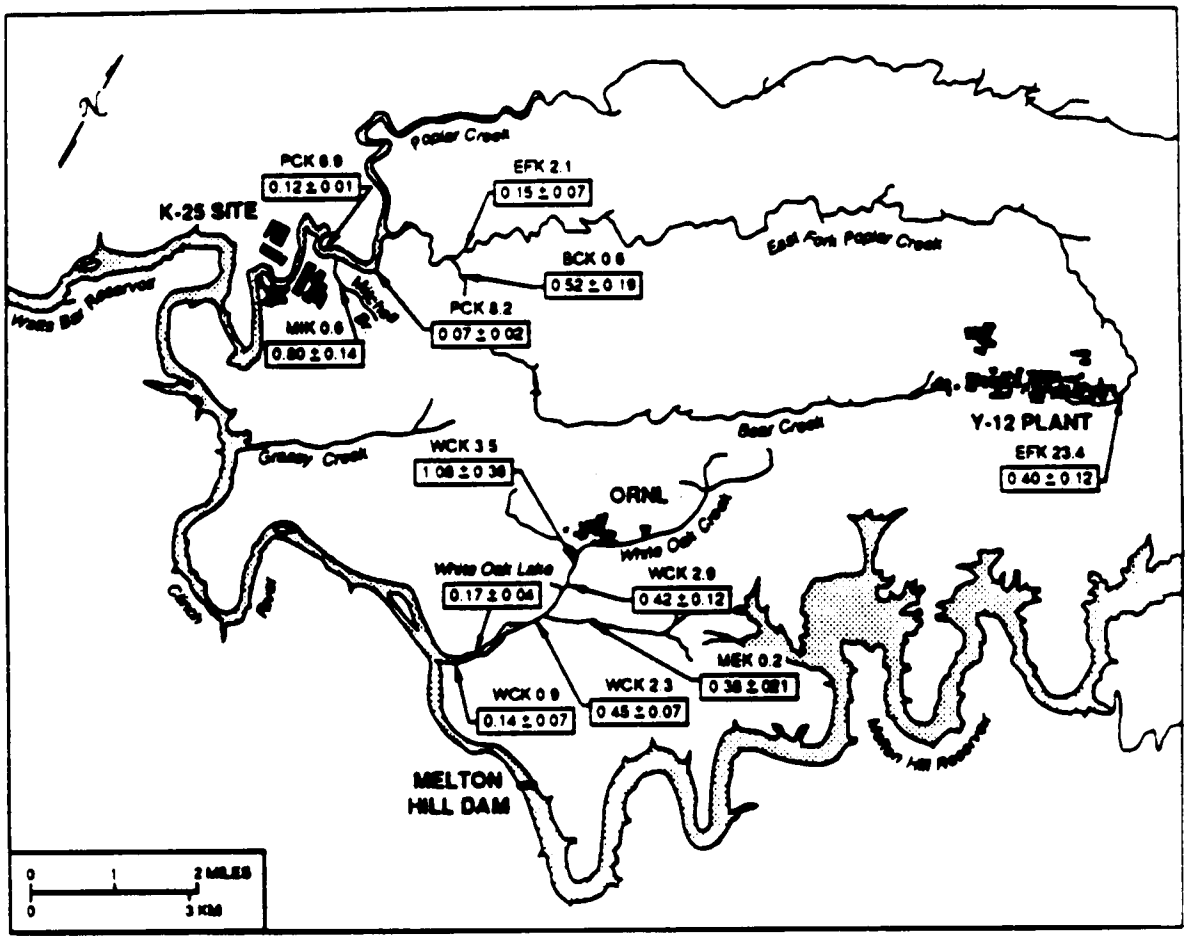

N
Poplar Creek
PCK 8.9
0.12 ± 0.01
EFK 2.1
0.15 ± 0.07
K-25 SITE
East Fork Poplar Creek
BCK 0.8
0.52 ± 0.19
PCK 8.2
0.07 ± 0.02
MIK 0.6
0.80 ± 0.14
Bear Creek
Y-12 PLANT
EFK 23.4
0.40 ± 0.12
Grassy Creek
WCK 3.5
1.08 ± 0.36
ORNL
White Oak Creek
White Oak Lake
0.17 ± 0.04
WCK 2.9
0.42 ± 0.12
MEK 0.2
0.38 ± 0.21
WCK 0.9
0.14 ± 0.07
WCK 2.3
0.45 ± 0.07
MELTON
HILL DAM
0 1 2 MILES
0 3 KM

Figure 6.

Case 1 : Assuming no behavioral effects

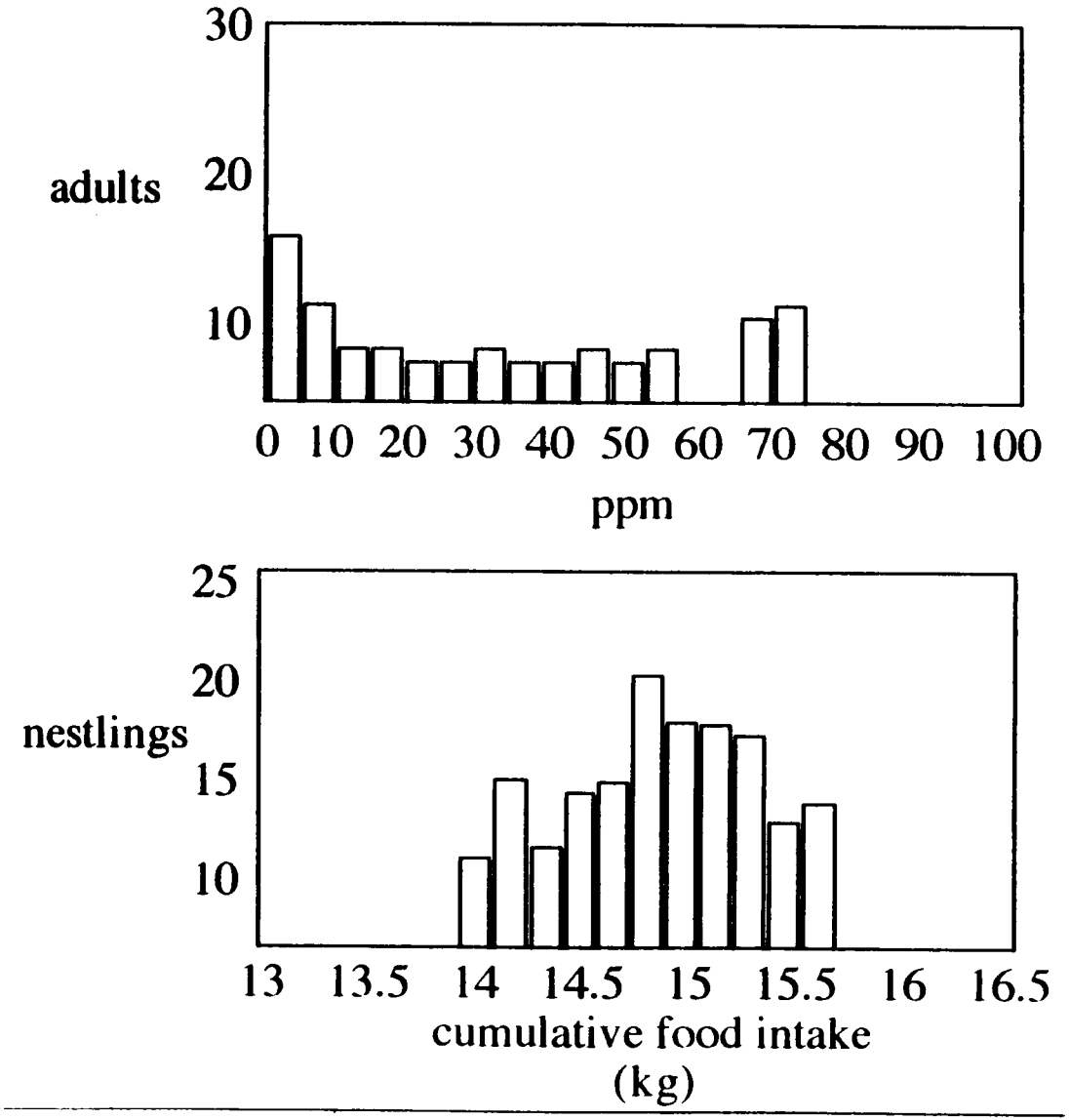


Figure 7.

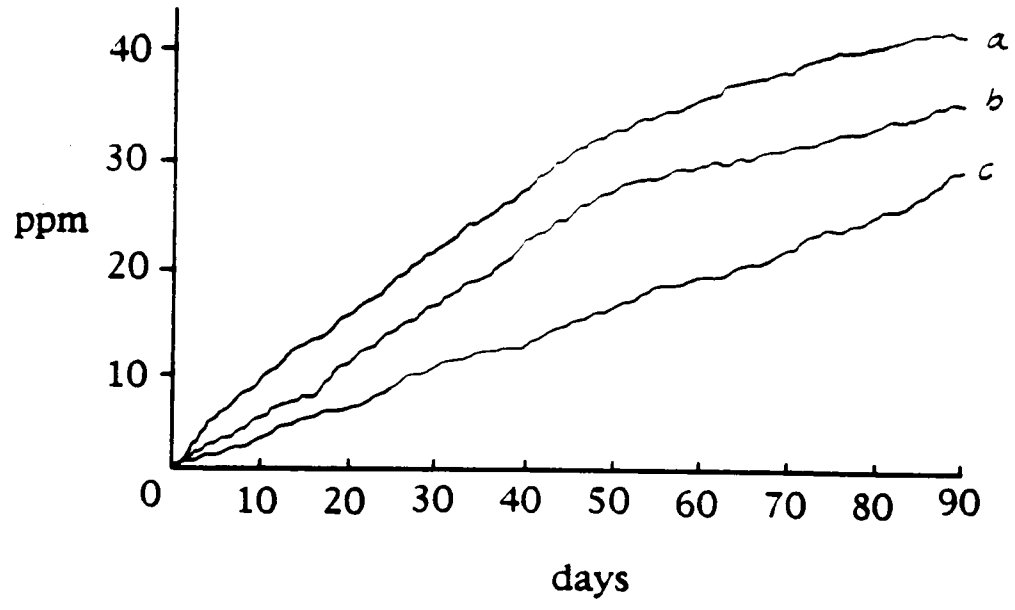


Figure 8.

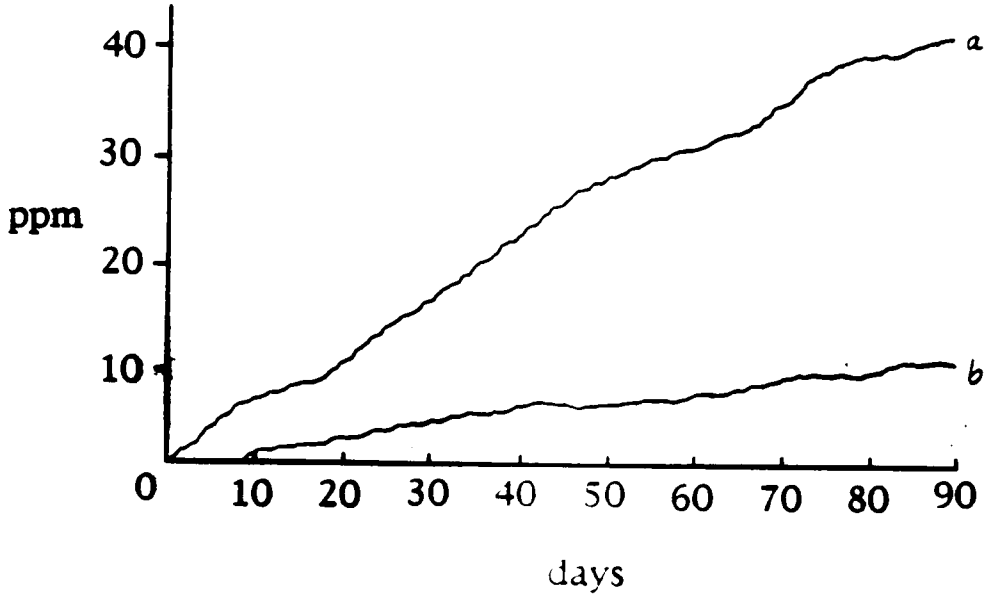
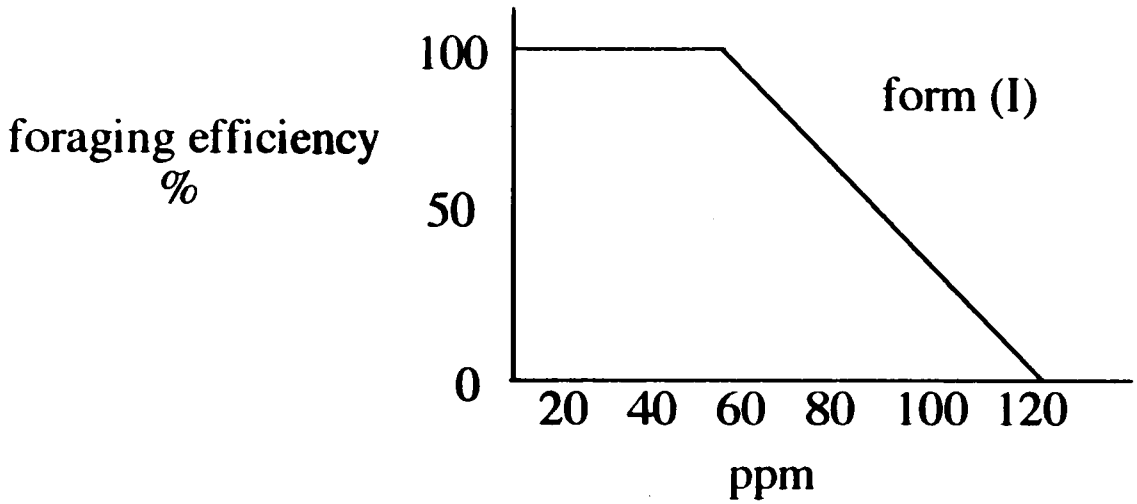


Figure 9.



100% foraging efficiency:

fish available (kg/cell)	uptake (50 gr)	time spent (15 min.)
5-10	1	1
10-15	2	2
15-20	4	3
20-25	8	4
25-30	10	4

Figure 10.

Case 2 : Assuming reduced foraging efficiency (form I)

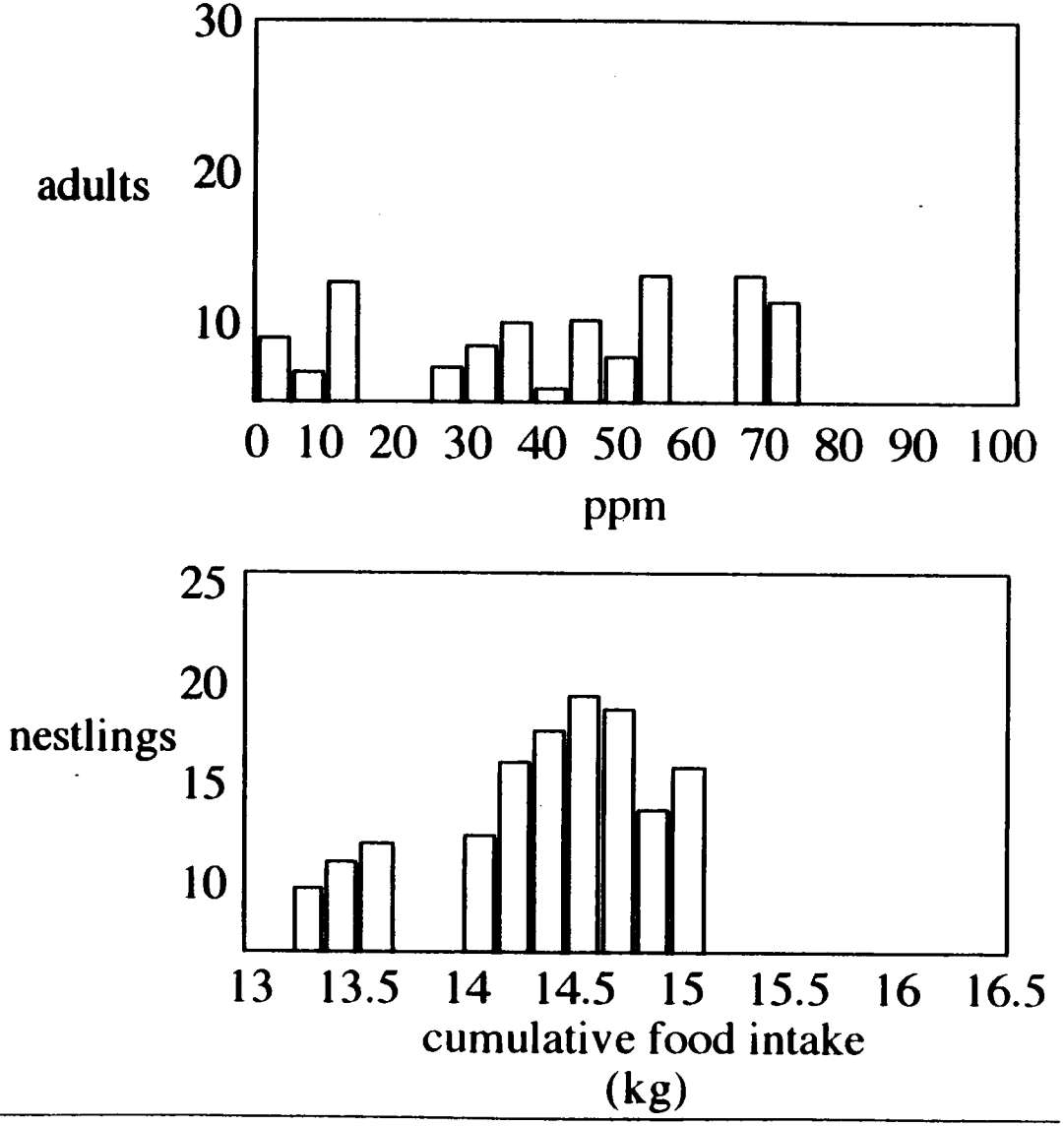


Figure 11

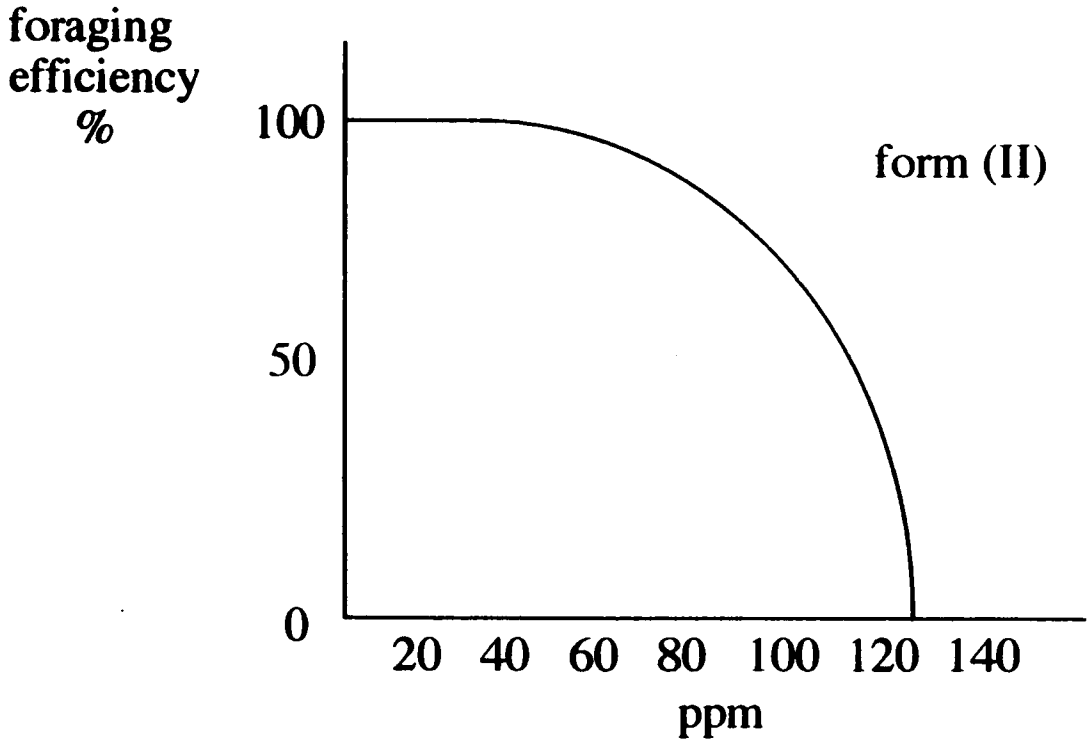

foraging
efficiency
%
100
50
0
form (II)
20
40
60
80
100
120
140
ppm

Figure 12

Case 3 : Assuming effect on foraging efficiency (form II)

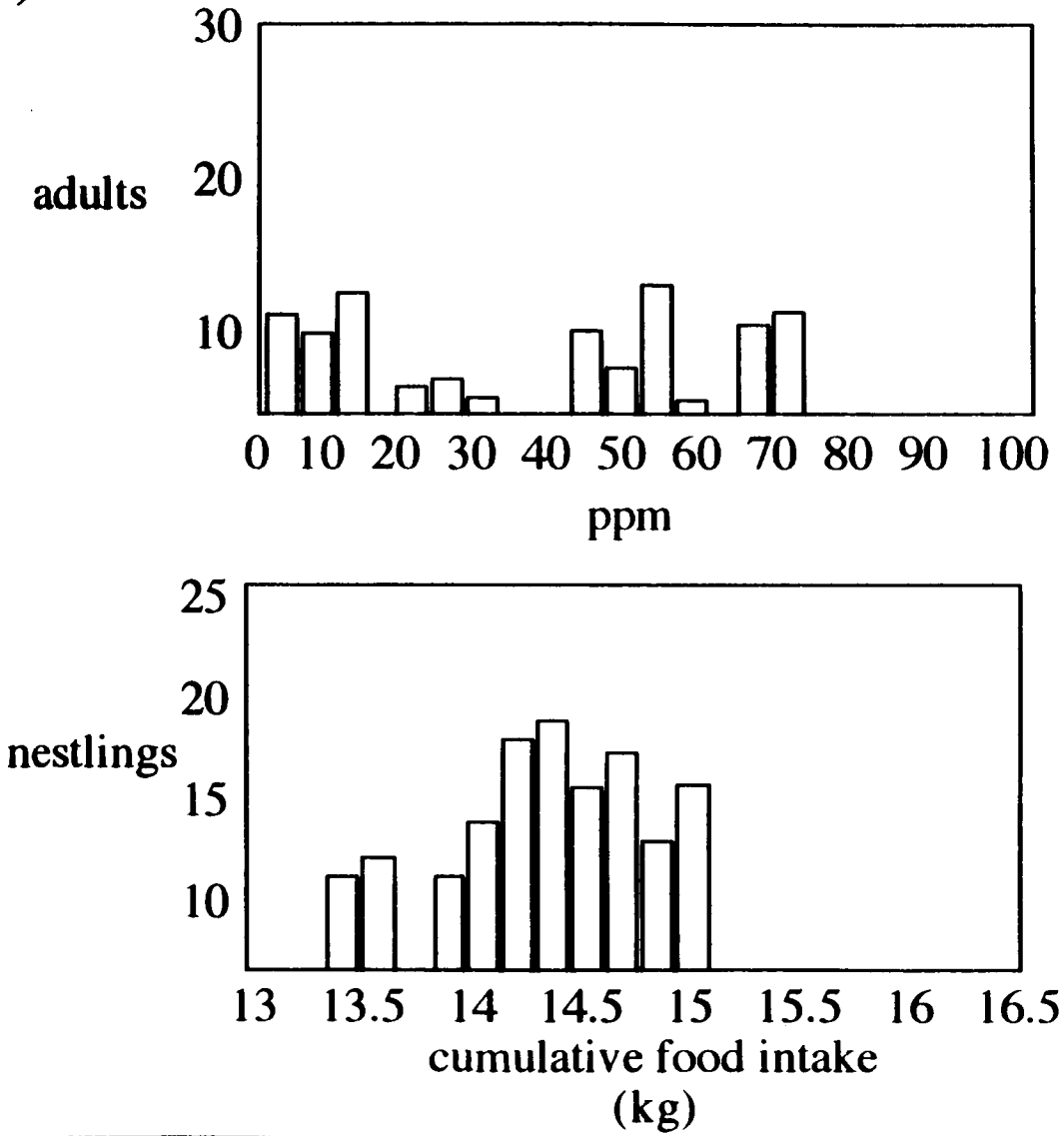


Figure 13

Effect on flight speed

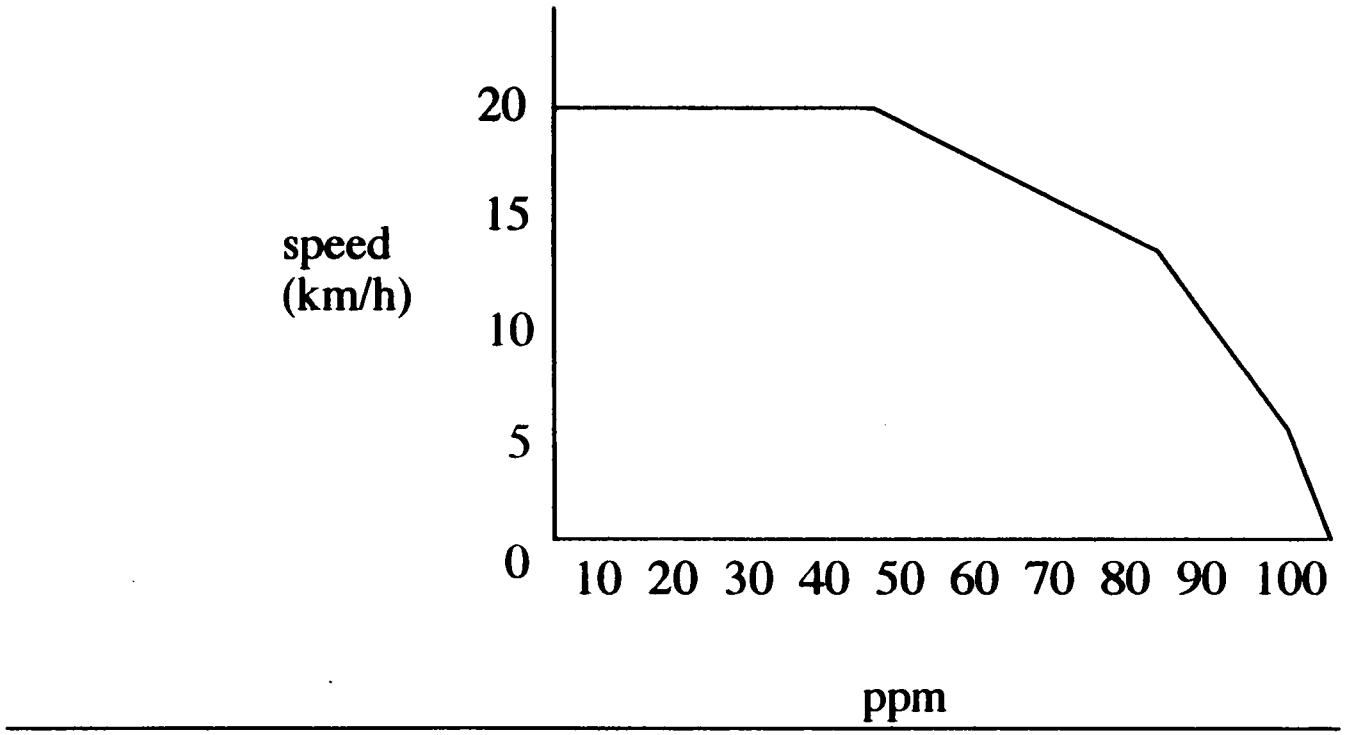


Figure 14

Case 4 : Assuming effects on flying efficiency

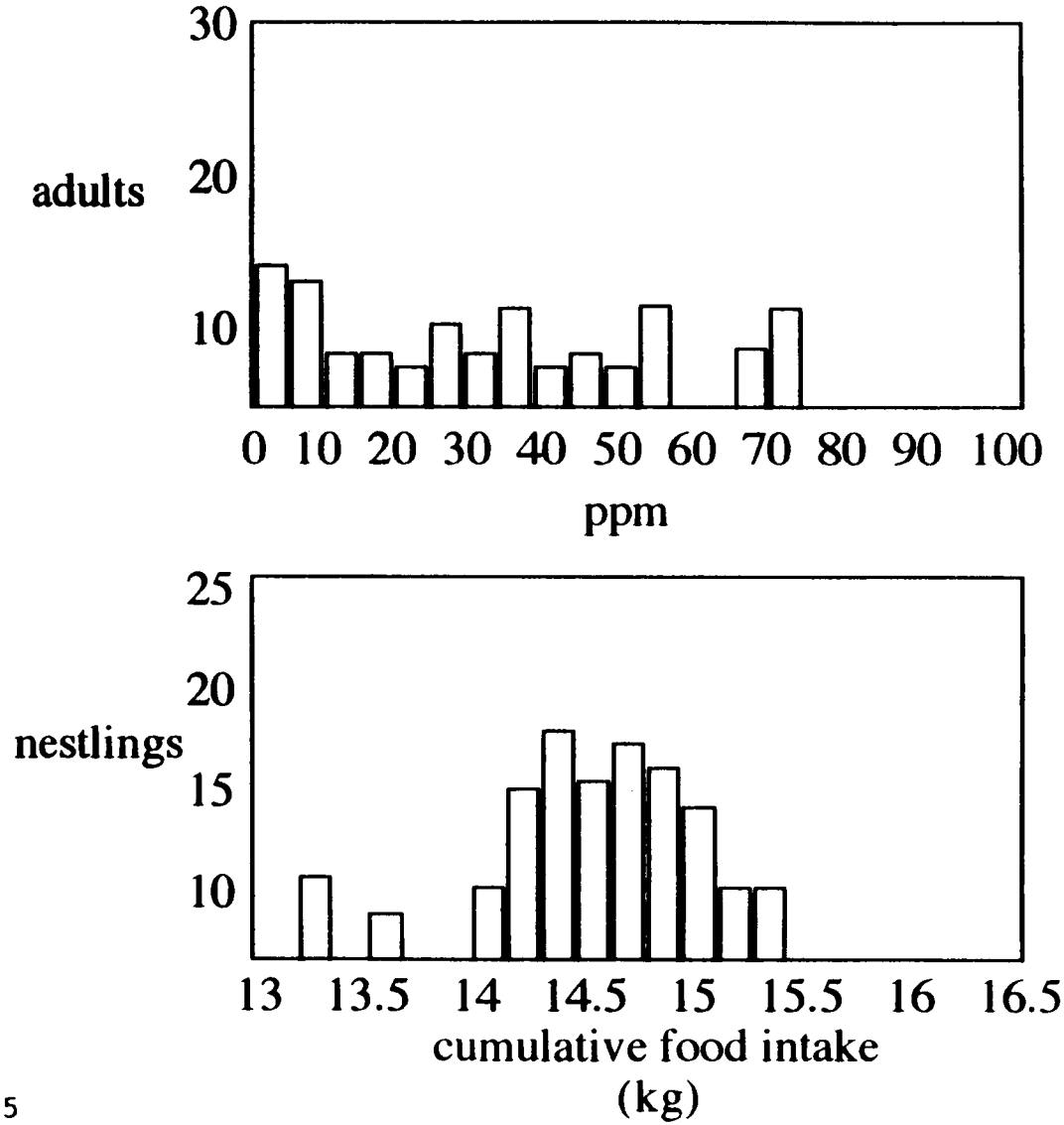


Figure 15

Case 5 : Assuming combined effects on foraging (form I) and on flying efficiency

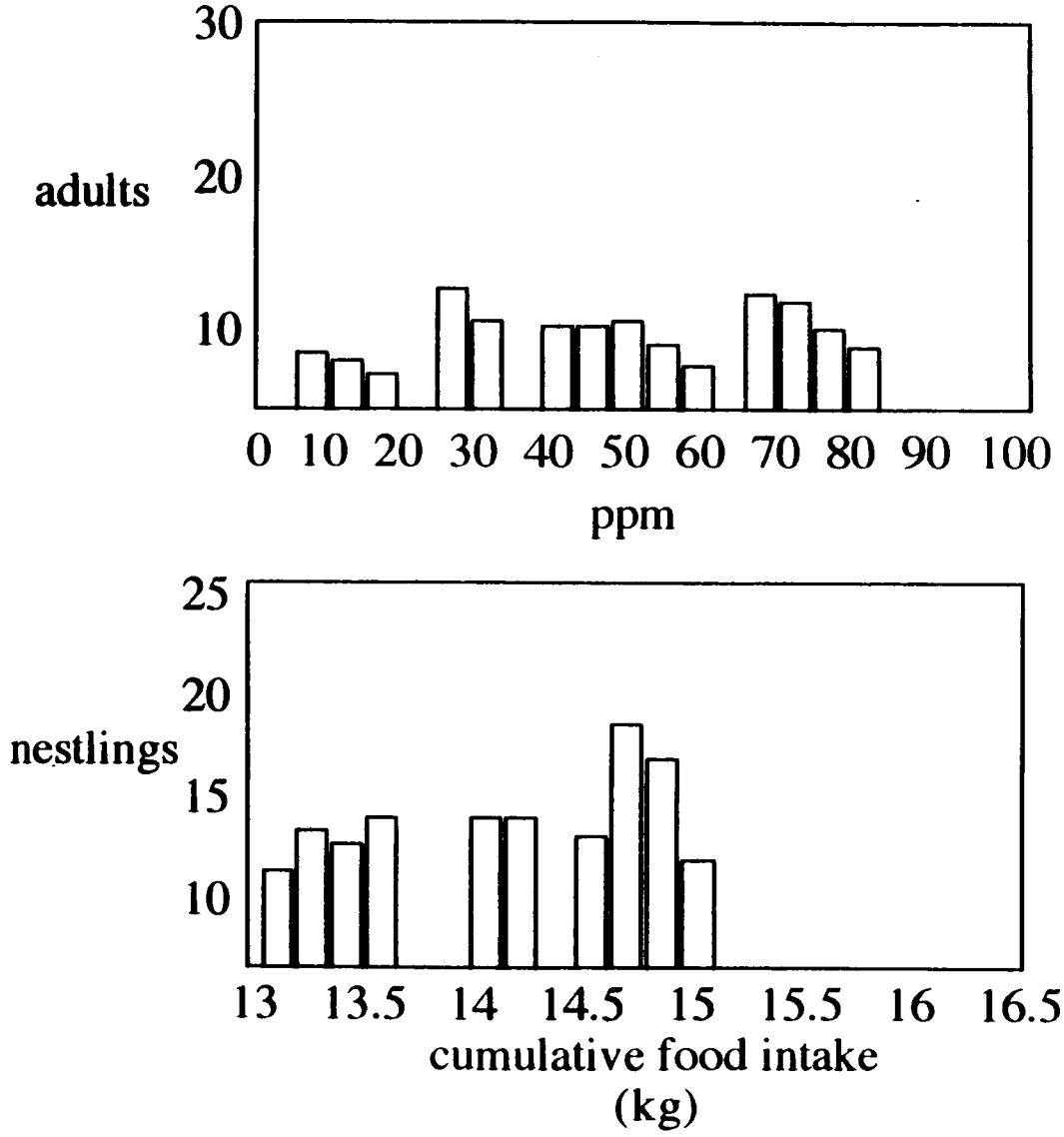


Figure 16

Case 6 : Assuming combined effects on foraging (form II) and on flying efficiency

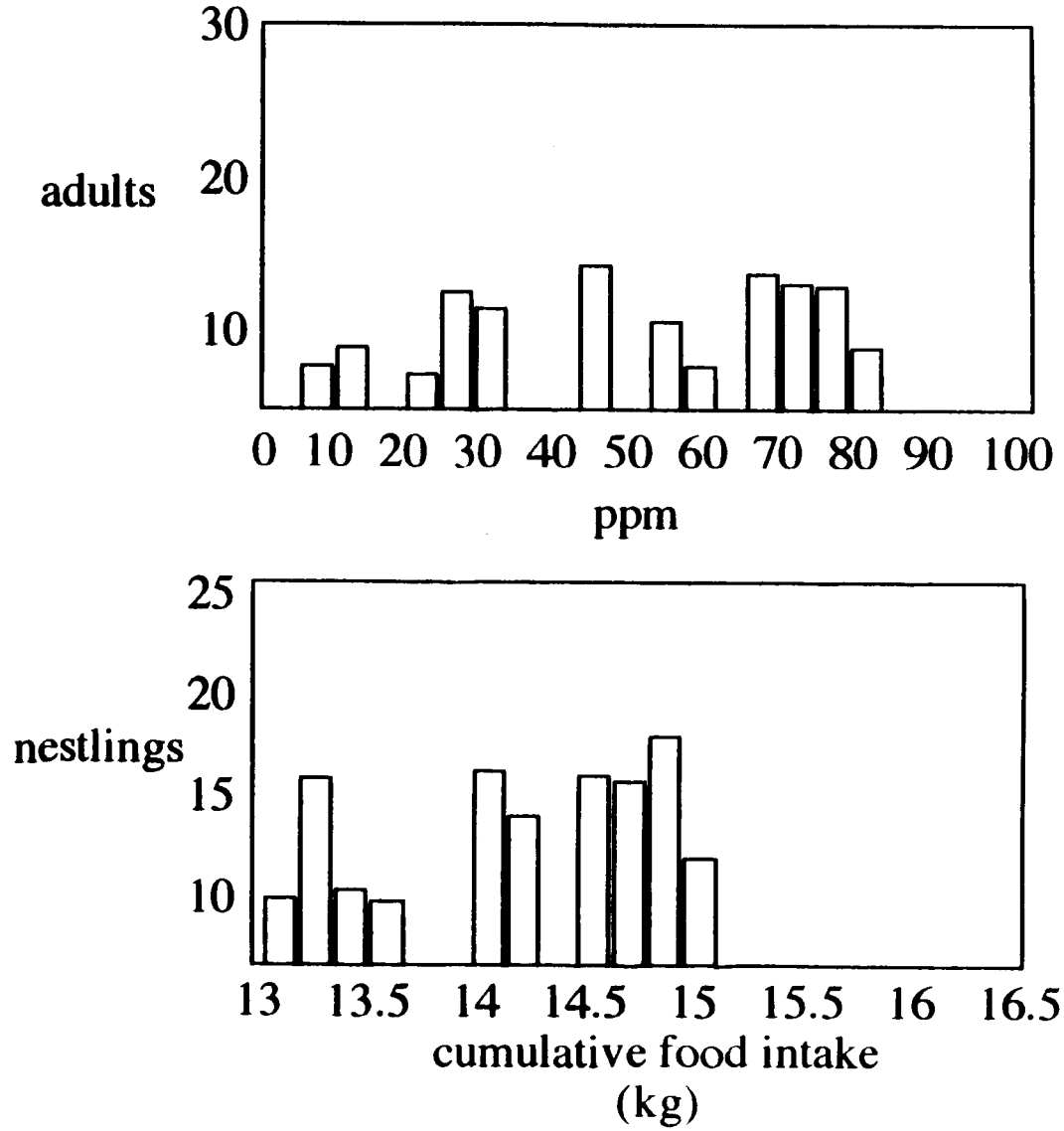


Figure 17

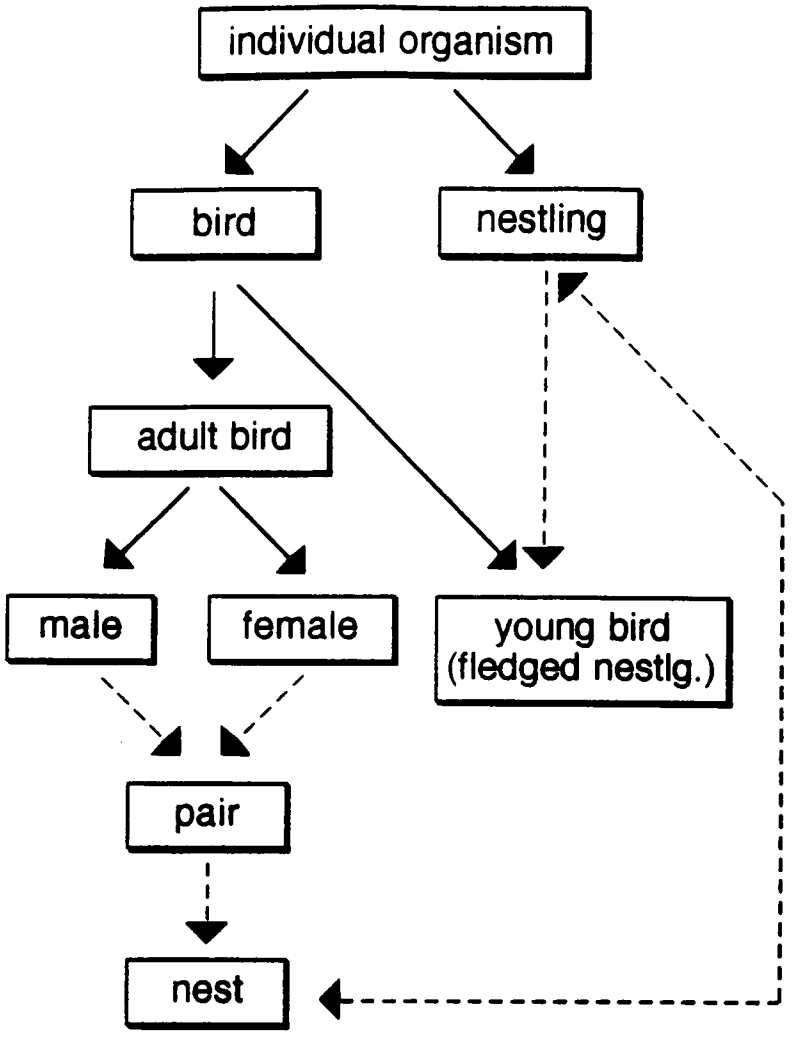

individual organism
bird
nestling
adult bird
male
female
young bird
(fledged nestlg.)
pair
nest

Figure 18

Table 1. Table of parameters

Parameter	Value	Units	Source
Daily need (max.)	0.2[a]	g/g-day	Kushlan
Metabolic rate (basal)	62	kcal/g-day	estimated[b]
Metabolic rate (free-living)	165	kcal/g-day	estimated[c]
Foraging distance from colony (max.)	7	km	Parnell et al, (1978)
Clutch size	3		Palmer (1962)
Incubation period	28	days	Bent (1926)
PCB assimilation efficiency	.92	---	calibrated (Fries, 1976)
PCB elimination rate	.006	day^{-1}	Bailey and Bunyan (1972)
Egg elimination rate	.012		estimated
Age at fledging	60	days	Hancock and Kushlan,1984)
Minimum food for fledging	14	kg	Kushlan (1976)
Max. PCBs (nestlings)	30	ppm	estimated

[a] Estimated using equation (Kushlan, 1986)
$\log(FI) = 0.966 \cdot \log(w) - 0.640$ FI (max. food ingestion rate g/day), w (weight, g)

[b] Estimated using equation (Lasiewski and Dawson, 1967)
$BMR = 77.6 wt^{0.723}$ BMR (kcal/day),w(g),t(day),

[c] Estimated using equation (Nagy, 1987)
$FMR = 4.797 wt^{0.749}$ FMR (kcal/day),w(g),t(day).

Table 2. Average PCB concentrations on adult birds under different uptake rates

Uptake rate (ppm)	Average PCBs conc. (ppm)	Standard Deviation
0.3- 0.5	19.3432	13.2332
0.5- 0.8	23.3424	15.3435
0.8- 1.1	28.0988	14.9497
0.0- 2.0[a]	55.9423	33.7823

VITA

Yiannis G. Matsinos was born in Athens, Greece on May 6, 1963. He graduated from Evangeliki School of Smyrni in June, 1981 and enrolled in the Mathematics School of the University of Athens pursuing a Bachelor's degree in Mathematics. He graduated in February of 1986 and in September of the same year he accepted a Teaching Assistantship at the University of Tennessee, Department of Mathematics for graduate studies leaading to the Ph. D. During his initial years at the university he enrolled in several ecology courses and subsequently made the decision to change his educational plans. He received a Master's degree in Mathematics in December, 1990, and enrolled in the Graduate Program in Ecology in January, 1991 after accepting a Research Assistantship working towards a Ph. D. in Ecology.

After passing his final examination in August, 1994, he will graduate on December of the same year. After a one year obligatory military service in Greece, he will be coming back to the United States to continue working on modeling of wading birds at the University of Miami.