MODELING ECOLOGICAL RISKS OF PESTICIDE APPLICATION: A REVIEW OF AVAILABLE APPROACHES

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EXECUTIVE SUMMARY

In 1992 an Ecological Fate and Effects Task Force within the EPA Office of Pesticide Programs issued a report that substantially revised the agency's approach to pesticide risk assessment. Among the most important recommendations from the Task Force was a recommendation to eliminate the field test as a routine component of the pesticide risk assessment process. As an alternative, the Task force recommended that initial decisions be based solely on laboratory test data. Where initial test data showed a potential for long-term effects, a refined assessment would be performed. Mitigating measures such reduced application rates, mandatory tillage practices, or changes in formulation could be implemented depending on the outcome of the refined risk assessment.

Modeling of ecological effects was specifically identified by the Task Force as a research need, to "predict and/or characterize adverse effects in non-target organisms, their populations and communities." This report provides a review of available modeling approaches that could meet this need, with an emphasis on new approaches to population modeling published in the scientific literature within the past five years. Four model types were reviewed: age/stage-structured models, individual-based models, metapopulation models, and spatially explicit models. Four criteria were used to evaluate the modeling approaches:

- ability to characterize ecologically relevant effects (e.g., the abundance and/or persistence of populations),
- ability to characterize the spatial and temporal distributions of exposures and effects.
- applicability to a variety of types of biota and exposure situations, and
- current degree of acceptance within the scientific community.

All four modeling approaches were found to be applicable within one or more phases of the New Paradigm. Age/stage-structured models appear most likely to be useful for initial registration decisions. For refined assessments (e.g., special reviews regional assessments)

the other three modeling approaches, because of their greater flexibility and ability to simulate realistic pesticide application regimes, may be more appropriate.

The review found that age/stage-structured models and metapopulation models are already extensively used in natural resource management and no further scientific development is needed to support use by EPA. Individual-based models and spatially-explicit models have appeared in the refereed scientific literature only within the past five years and have had few management applications. Although in the long run these approaches may well be the most useful, substantial research and development are still needed to support regulatory use by the Agency.

Four steps were identified that EPA could take to increase the use of population models in pesticide risk assessment:

- Broaden the management basis for decisions concerning pesticides to include measured and effects on populations
- Develop reference population data sets for representative species and local environments
- Demonstrate new models through application in actual assessements
- Fund research in individual-based and spatially-explicit modeling, including the support of graduate and postgraduate fellowships
- Train agency staff in the theory and application of population models

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1.0 INTRODUCTION

In 1992 an Ecological Fate and Effects Task Force within the EPA Office of Pesticide Programs issued a report that substantially revised the agency's approach to pesticide risk assessment. Prior to 1986, the agency had operated under a tiered approach that included mesocosms and field tests (Urban and Cook 1986). The first tiers involved simple acute toxicity tests and exposure criteria using the "quotient approach." Estimates of standard toxicity test endpoints such as $LC_{50}s$ and $LD_{50}s$ were compared directly to Estimated Environmental Concentrations (EECs) derived from standardized surface-water runoff models. If the quotients exceeded specified Levels of Concern (LOCs) then more extensive testing (more species, full life-cycle tests, reproduction tests) would be required. If these tests showed the pesticide to be safe, then no further testing was required. If there was still uncertainty concerning the effects of the pesticide, then mesocosm or field tests could be required prior to decision making.

In theory, mesocosm and field tests were supposed to provide information on long-term, chronic, population and ecosystem-level effects of pesticide use under realistic application conditions. In practice, data obtained from these tests proved to be difficult to use in regulatory decision making. The systems were difficult to standardize and replicate, and were expensive to use. The Task Force found that mesocosm/field data were adding little to the information available for regulatory decision making, and were adding greatly to the time and money required to make decisions. Consequently, the Task Force recommended eliminating the field test as a routine component of the pesticide risk assessment process. As an alternative, the Task force recommended that initial decisions be based solely on laboratory test data. Where initial test data showed a potential for long-term effects, mitigating measures such as reduced application rates, mandatory tillage practices, or changes in formulation would be implemented.

The Task Force's recommendations were formalized in an "Implementation Paper for the New Paradigm" issued in 1993. This document defined the paradigm to consist of the following components (SETAC 1994, Appendix B):

- **Risk assessment** is the scientific phase of the overall process and consists of hazard identification, and exposure assessment, ultimately integrating hazard and exposure to characterize risk.

- **Risk mitigation** involves mitigation measures to reduce or eliminate source contamination and adverse environmental impact.

- **Risk management** is a policy-based activity that defines risk assessment questions and endpoints to protect human health and ecological systems. It takes the scientific risk assessment and incorporates social, economic, political, and legal factors, which impinge or influence the final decision and selects regulatory actions.

The New Paradigm emphasizes early decision making and mitigation. For new registrations, the paradigm employs essentially the same tier-1 LOCs that were used in the old assessment scheme. If these levels are not exceeded, then registration may proceed. If they *are* exceeded, then a "refined risk assessment" must be performed, and potential mitigation measures must be identified. Costs and benefits of the mitigation measures must be evaluated.

Specific procedures for performing refined risk assessments and evaluating benefits of mitigation were not specified in the implementation paper and are still to be defined. Modeling of ecological effects was specifically identified as a research need, to "predict and/or characterize adverse effects in non-target organisms, their populations and communities." This report provides a review of available modeling approaches that could meet this need, with an emphasis on new approaches published in the scientific literature within the past five years.

1.1 Endpoints

FIFRA requires decisions to incorporate analysis of risks and benefits of regulatory decisions. If a pesticide is to be restricted, it must be shown that reductions in risks to ecosystems will outweigh economic benefits of unrestricted use. Ecological endpoints in the

past have emphasized (1) predicted effects on individual exposed organisms, and (2) observed fish and bird kill incidents. However, neither predicted effects on individuals nor enumerations of kill incidents can provide scientifically rigorous or defensible estimates of the benefits of regulation. All organisms die. Except in the case of threatened or endangered species, the abundance and persistence of populations are a more relevant endpoint. Ecological risk assessments for pesticides would be more useful and scientifically credible if it were possible to base decisions on risks to populations rather than risks to individuals, and to consider both *spatial scale* and *temporal scale* in the assessment. If only a small fraction of a population is exposed, or if the population recovers rapidly after exposure events, risks associated with pesticide use may be small even if lethal exposures occasionally occur. Some pesticides are acutely toxic (e.g., neurotoxins in birds) but not persistent in the environment. Such substances are arguably preferable to persistent pesticides that have long-term chronic effects on avian reproduction that might only be detected after substantial environmental damage has occurred. If it were possible to estimate the spatial variations in pesticide exposure and to evaluate the rate of recovery of exposed populations, this information could be used to design pesticide application regimes that would minimize ecological risks.

1.2 Model Evaluation Criteria

None of the above considerations are captured in the tier-1 assessment criteria. However, they could be included in "refined risk assessments," if appropriate models could be found that extrapolate effects on individual organisms (mortality, reproduction etc.) to effects on populations and ecosystems. Are there models available that can, in principle, be used for this purpose? What additional research or demonstration is required before they can be used within the new paradigm? The following criteria were used in this report to evaluate the potential utility of the modeling approaches reviewed:

Endpoints: ability to characterize ecologically relevant effects, i.e., the abundance and/or persistence of populations.

Spatiotemporal resolution: ability to characterize the spatial distribution of exposures and effects; ability to account for variations in temporal exposure over a period of days, weeks, or months.

Generality: applicability to a variety of types of biota and exposure situations relevant to pesticide risk assessment.

Current degree of acceptance: degree of acceptance within the scientific community, as evidenced by the number of successful applications (e.g., in resource management or conservation biology), and the number of refereed publications that employ the approach.

"Data requirements" and "data availability" were not included as evaluation criteria, because within each of the major categories of modeling approaches one can find models possessing a wide a range of data requirements and availabilities. It is almost always possible to adjust a model to fit the available data.

1.3 Past Reviews

There have been several recent reviews of models potentially useful in ecological risk assessment for chemicals and pesticides. Barnthouse et al. (1986) reviewed the general history of successes and failures of population and ecosystem theory in resource management and environmental impact assessment. Emlen (1989) reviewed general types of theoretical population models with regard to applicability to terrestrial ecological risk assessments. Both of these reviews concluded that age-structured population models, i.e., models of populations that categorize organisms in terms of age and reproductive status, have been widely used in fish and wildlife management, have been validated under many circumstances, and are ready for use in ecological risk assessment of chemicals and pesticides. The widely-used population modeling program RAMAS (Ferson and Akcakaya 1989; Ferson 1990) is an age-structured population model. Barnthouse (1993) provided a discussion of the historical development and basic principles of age-structured population models, with a review of the literature and specific examples of applications to toxic chemicals. Barnthouse (1992)

highlighted several new developments, specifically in landscape modeling and individual-based modeling that appeared potentially useful for ecological risk assessment.

There is no need to repeat these reviews. Most of the literature reviewed was published prior to 1990. The age/stage-structured models emphasized by Emlen (1989) and Barnthouse (1993) are refinements and applications of a theory that is more than 50 years old. These reviews should be consulted for detailed accounts of the historical development and underlying theory of population models. The following kinds of models are included in this review:

Age/stage-structured population models : These models subdivide populations into discrete classes based on age, size, sex, or reproductive status. The best-known model of this type is the Leslie Matrix (Leslie 1945). In this model information on the age-specific reproductive rates and probabilities of survival can be used to project the future growth or decline of the population and to show how the future status of a population should change in response to changes in survival and reproduction. Variants on age-structured models have been principal tools in natural resource management, especially for fish, since the 1950s. The matrix representation of population dynamics is highly flexible and has been modified variously to accommodate stochastic environmental variation, density-dependent survival and reproduction, and other biological or physical processes. The model can be formulated in terms of the size rather than the age of organisms. Caswell (1989) provided a thorough discussion of the theoretical development of these models. Applications through 1990 were reviewed by Barnthouse (1993). The discussion in this report will be limited to a few innovations that have appeared in the literature since 1990.

Individual-based models: Individual-based models are models that characterize the dynamics of populations in terms of the physiological, behavioral, or other relevant properties of the individual organisms. The "core" of an individual-based population model is a model of the organism, including its physiology, behavior, reproduction, spatial location, or any other relevant property. For some simple models, the population-level consequences of

individual properties can be generated analytically (e.g., Kooijman and Metz 1984, Hallam et al.1990). For more complex organisms or realistic environmental scenarios, these properties are calculated by numerical simulation: a fixed number of individuals are simulated day-by-day or week-by-week and quantities such as abundance, spatial distribution, or probability of extinction are generated by tabulating the numbers and distributions of organisms. Most of the published examples of individual-based organisms involve forest composition (Huston and Smith 1987, Shugart 1984, Dale and Gardner 1987), Cladocera (McCauley et al. 1990, Gurney et al. 1990, Hallam et al. 1990) or fish (Beyer and Laurence 1980), DeAngelis et al. 1991, Madenjian and Carpenter 1991, Rose and Cowan 1993). More recently, models that simulate the behavior and distribution of animals moving over a complex landscape have been developed (Loza et al. 1992, Liu 1993).

Metapopulation models: As discussed by Hanski and Gilpin (1991), a metapopulation can be defined as a "set of populations that interact via individuals moving among populations." Levins (1969), performed the first quantitative analysis of conditions under which a species consisting of many populations could remain extant even though individual populations were frequently fluctuating and going extinct. Many metapopulation models, including complex ones involving interacting species (e.g., hosts and parasitoids, predators and prey, plants and herbivores) have been developed for use in biological pest control studies (Murdoch et al. 1985). Many recent applications are in conservation biology, most notably in studies of the Northern spotted owl (Lande 1987, Lamberson et al., 1994) and other endangered species with fragmented spatial distributions (Lindenmayer and Lacy 1995). Hanski and Gilpin (1991) provided a good recent review.

Spatially-explicit models: Spatially-explicit models are models that incorporate realistic features of landscape structure. These representations can range from idealized arrangements of "patches" of suitable and unsuitable habitat (Lamberson et al. 1994) to vegetation maps generated by Geographic Information Systems (GIS) (Pulliam et al. 1992, Liu 1993, Turner et

al. 1993). These models can be thought of as extensions of the metapopulation and individual-based modeling concepts to complex spatial environments.

2.0 DESCRIPTION OF MODELING APPROACHES

This section provides detailed descriptions of a few recent models of each type, drawn from the recent peer-reviewed literature. The objective of these descriptions is to provide a foundation for evaluating the consistency of each approach with the evaluation criteria and for determining the potential applicability of each within the New Paradigm.

2.1 Age/Stage-structured Models

Both Emlen (1989) and Barnthouse (1993) noted that age/stage-structured population models, i.e., models in which all organisms belonging to a population are classified into groups according to age, size, and reproductive status, have a long history of application in natural resource management. These models are the most readily available quantitative methods for assessing risks of toxic chemicals to populations. The simplest such model assumes that (1) all organisms of the same age are identical, (2) all rates of birth and death are constant and independent of environmental variation, and (3) the rate of population growth is independent of population size:

$$\sum_{x=1}^{n} \lambda^{-x} l_x m_x = 1$$

(1)

where

l_x = fraction of organisms surviving from birth to age x

m_x = fecundity of individuals at age x

λ = finite rate of natural increase

Provided that l_x and m_x remain constant, any population growing according to equation 1 will assume a stable age distribution in which the fraction of organisms in each age class x will remain the same from each generation to the next. Once the stable age distribution is achieved, the population will either grow or exponentially according to the following equation:

$$N_t = N_0 \lambda^t \tag{2}$$

where

N_0 = population size at time 0

N_t = population size at time t

The above model is biologically unrealistic in many ways, however, it has been successfully applied to many population management problems and is still the most widely-applied approach to assessment of the impacts of human activities on the abundance and persistence of fish and wildlife populations.

Leslie (1945) developed a matrix form of equation (2) that permits detailed analysis of the influence of age-specific survival and reproduction rates on the rate of population growth:

$$N(t) = LN(t-1) \tag{3}$$

where $N(t)$ and $N(t-1)$ are vectors containing the numbers of organisms in each age class (N_0,... N_k and L is the matrix defined by

$$L = \begin{bmatrix} s_0 f_1 & s_1 f_2 & s_2 f_3 & \cdots & s_{k-1} f_k & 0 \\ s_0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & 0 & \cdots & 0 & 0 \\ 0 & 0 & s_2 & \cdots & 0 & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & \cdots & s_k & 0 \end{bmatrix} \tag{4}$$

where

s_k = age-specific probability of surviving from one time interval to the next and

f_k = average fecundity of an organism of age k

As discussed by Barnthouse (1993), a wide variety of population models can be derived from equation 4 by making the survival and reproduction parameters random variables or functions of environmental parameters or population size. The model can be defined in terms of sizes or life stages rather than ages. Caswell (1989) presents a detailed discussion of the mathematical properties of all of these models. Barnthouse (1993) and Emlen (1989) described the range of resource management and risk assessment applications to which age/stage-structured models have been applied. Some of these applications involve pesticides and toxic chemicals (e.g., Tipton et al. 1980, Samuels and Ladino 1983, Barnthouse et al. 1990). The literature search performed for this report revealed no qualitatively new types of age/stage-structured models.

Some new research has, however, been published concerning methods for comparing the influence of different life-history characteristics on the rate of population growth (λ). The term elasticity(e_{ij}) (deKroon et al. 1986) has been applied to a measure of the proportional sensitivity of λ to each element of the population transition matrix (a_{ij}):

$$e_{ij} = (a_{ij}/\lambda)(\partial\lambda/\partial a_{ij}) \tag{5}$$

Elasticities as defined by equation 5 measure the relative contribution of each life-cycle element to the population growth rate. They have been found useful in theoretical studies of the relative fitness of different life-history strategies, especially for organisms such as plants that have extremely complex life histories compared to most vertebrate animals. Refinements of the basic methodology have been described by van Groenendael et al. (1994) and van Tienderen (1995). Meyer and Boyce (1994) used elasticity to compare the influence of changes in fecundity and survival due to hypothetical pesticide exposures on bird populations with different age and size-structures.

The elasticity methodology itself does not provide any new approaches for modeling impacts of pesticides on populations. It may, however, be useful in the design of model-based assessment schemes. Models representative of a range of life-history types (small, fast-growing, short life-span vs. large, slow-growing, long life-span) would be developed. Elasticity analyses would be used to identify the life-cycle stages most strongly influencing the long-term population growth rate. These are the life stages at which pesticide exposure would be likely to have the greatest impacts.

2.2 Individual-Based Models

As the term implies, individual-based models provide the opportunity to evaluate the influence of characteristics of individual organisms on the abundance of whole populations. Age- and stage-based models already account for the influence of age and (for some stage-based models) size on population dynamics, but individual-based models can expand the list of characteristics considered to *any* aspect of organismal biology believed to be relevant. For the purposes of pesticide risk assessment, the most relevant of these appear to be physiology and behavior. The general procedure is to develop a model of the individual organism to whatever level of detail is required, and then to infer the properties of the population as a whole either by analytical solution of equations or by numerical simulation of the activities of hundreds or thousands of individual organisms.

Physiological characteristics included in individual-based models have emphasized metabolism, growth and contaminant pharmacodynamics. Work on metabolism was

pioneered by Kooijman and Metz (1984), who examined the influence of contaminants on metabolism and population growth using *Daphnia* as a model organism. Hallam and Lassiter (Hallam et al. 1990, Lassiter and Hallam 1990) extended this approach to include (1) a thermodynamically-based model of the uptake of contaminants from aqueous media and (2) a definition of death in terms of the internal dissolved contaminant concentration within an organism. McCauley et al. (1990) and Gurney et al. (1990) developed an energetics-based model of *Daphnia* growth and reproduction and used the model to predict time-dependent changes in the age and size-structure of *Daphnia* populations in response to changes in food availability.

All of the above models were developed for aquatic organisms with relatively simple life-cycles. The emphasis in model analysis was on evaluation of general properties of the models through analytical investigation of the equations. DeAngelis et al. 1991 and Rose and Cowan (1993) developed models of fish populations that include metabolism, growth, foraging behavior, and prey selection as functions of the life stage and age of the fish. DeAngelis et al. (1991) even included the nesting and nest defense behavior of male smallmouth bass. The approach followed in developing both of these models was to use the existing extensive theoretical literature on bioenergetics, reproduction, and foraging of individual fish, coupled with exhaustive evaluation of the life history of specific fish species, to develop detailed models of each life-stage from egg through reproductive adult. Population-level consequences of changes in the physiology, behavior, or reproduction of individual fish are inferred by brute-force simulation of the birth, growth, and death of hundreds or thousands of individual fish. The models are calibrated to extensive data sets collected for specific fish populations.

The model of DeAngelis et al. (1991), for example, simulates the spawning, growth, and survival of a year-class of smallmouth bass (*Micropterus dolomeui*) in Lake Opeongo, Ontario. It is structured as a set of discrete submodels that simulate the daily activities and physiological condition of each individual fish in the model population. Reproductive behavior in smallmouth bass is quite complex. Adult males excavate nests, and after eggs are deposited in the nests the males defend the nests from predators for several weeks while the

eggs hatch and develop through their early larval stages. Spawning behavior and spawning success have been shown to be both temperature and size-dependent. Larger males spawn earlier; larvae that are spawned early have a size advantage over larvae that are spawned late. Success in rearing a brood has also been shown to be related to the size and condition of the guarding males. The males do not feed during the brood period; smaller males and males in poorer condition at spawning abandon their nests much more frequently than do larger, healthier males. Environmental conditions also have an important influence on spawning success because storm events that cause water temperatures to fall below a critical threshold cause the males that have spawned to abandon their nests.

The model of DeAngelis et al. (1991) simulates all of these processes. Given an initial size/condition distribution of males and a specified daily temperature regime, the model simulates the nesting and brood-rearing success of each male over the course of the reproductive season. The probability of successfully rearing a brood and the number of young fish produced from each brood are defined as probabilistic functions of the size and condition of the male at the time of nesting.

Growth and survival of the young-of-the-year fish is simulated on a daily time-step. The model incorporates well-established models of fish bioenergetics and foraging. Prey abundances and size distributions are specified in the model; the prey selectivities and feeding successes of each fish are specified through established predation models that account for the swim speed and visual acuity of the fish (both dependent on size) and on the frequency of encounter with prey of appropriate sizes. All of these processes are stochastic. Rather than producing single numbers for the abundance and average size of fish, the model produces, each day, a size and age (in days) distribution of fish. It is possible to calculate the relative probability of survival of larvae spawned on any given day or having any given initial size.

The objective of DeAngelis et al. (1991) was to understand and explain the processes responsible for recruitment success in smallmouth bass: why more fish are produced in some years than in others and why large males spawn earlier than small males in spite of the increased risk of low-temperature events. Because of the physiological detail included in the

model, however, it would be relatively easy to modify it to include lethal and sublethal effects of toxic chemicals.

Individual-based models have also been applied to terrestrial biota. In many cases the emphasis has been on behavior rather than metabolism and physiology. Pulliam et al. (1992) developed a model of the Bachmann's sparrow population on the Savannah River Site, South Carolina, derived from the individual foraging behavior and habitat selection of the birds (this model is discussed in detail in section 2.4).

Lacy (1993) described a generalized computer program (VORTEX) that simulates the local population dynamics of terrestrial vertebrate populations. VORTEX was intended for use in the management of small populations threatened by habitat loss, environmental variability, and loss of genetic variation. The core of VORTEX is stochastic model of the birth, growth, reproduction, and death of each individual animal. At the start of simulation, an initial number of animals, age/sex structure, genetic composition, and carrying capacity are specified. At each subsequent time-step (normally one year, but modifiable by the user), mature animals mate and produce young. The percentage of mature females producing young in a given year, and the number of young produced by each reproducing female, are drawn from probability distributions. Several different options are available to specify mate selection and, thus, inbreeding effects. Following reproduction, the individual animals are randomly "killed" according to numbers drawn from age-specific probability distributions. Both reproduction and survival are assumed to be density-dependent, with expected values changing depending on the relationship between the current population size and the carrying capacity. Reproduction and survival are subject to two sources of environmental variation: "normal" annual variation specified by a binomial probability distribution, and "catastrophic" variation that occurs randomly according to a uniform probability distribution. When catastrophes occur, survival and reproduction rates of all animals are reduced by a constant fraction specified by the user.

Each simulation "run" produces a single stochastically-determined time-series of population sizes and age/sex/genetic compositions. The simulated population either persists throughout the simulation or goes extinct at some point during the simulation. Estimates of

the probability of persistence and expected time-to-extinction of the simulated populations are obtained by performing multiple runs (hundreds or thousands); the results of these simulations can be summarized as (1) probability of extinction as a function of simulation time, (2) median and mean time to extinction of populations that go extinct, and (3) mean size and genetic variation within populations that survive.

VORTEX, in the version described by Lacy (1993), can simulate up to 20 populations, between which immigration and emigration can occur. In this form it can be viewed as a metapopulation model (see section 2.3). VORTEX has been applied to a variety of endangered bird and mammal species (Lacy et al. 1989, Seal and Foose 1989, Seal and Lacy 1989, Lacy and Clark 1989, Maguire et al. 1990, Foose et al. 1992, Lindenmayer et al. 1993). VORTEX, unlike the model of DeAngelis et al. (1991) does not explicitly simulate ecological or physiological processes relevant to pesticide exposure and effects assessment. However, information concerning(1) the distribution of doses within an exposed population and (2) dose-response relationships for reproduction and mortality could be used to modify the survival and reproduction functions used in VORTEX.

2.3 Metapopulation Models

Most species do not exist as continuous interbreeding populations. They consist of subpopulations inhabiting patches of suitable habitat mixed in with patches or regions of unsuitable habitat. All are subject to environmental variability that may be either large or small. Small populations frequently go extinct, but habitat patches are then recolonized by colonists arriving from other patches. This view of species as "metapopulations" was first formalized by Andrewartha and Birch (1954), although they did not use the term. The first quantitative studies or metapopulation biology were published in the 1960s by MacArthur and Wilson (1967) and den Boer (1968). Levins (1969) is credited with developing the first formal model to specifically address the central question in metapopulation biology: how are (1) the fraction of occupied patches and (2) the expected time to extinction of the species as a whole affected by the probabilities of extinction and recolonization of individual patches?

Levins (1969) formulated a simple relationship between the fraction of habitat patches occupied by a species at any given time ($p(t)$), the rate of extinction of occupied patches (e), and the rate of production of propagules from each occupied patch (m). He reasoned that at any time t, mp propagules would be produced. Assuming equal probability of dispersal to occupied and unoccupied patches, a fraction equal to ($1-p$) of these would colonize unoccupied patches. At the same time, a total number of patches equal to ep would become extinct. The rate of change in p at any time would be determined by the equation:

$$dp/dt = mp(1-p) - ep \qquad (6)$$

It follows from this equation that the equilibrium frequency of occupied patches (p^*) is determined by the ratio of the extinction (e) and colonization (m) rates:

$$p^* = 1 - e/m \qquad (7)$$

It is intuitively obvious even without Levins' model that if extinction is more likely than dispersal (i.e., e is larger than m) the species must become extinct. It is not, obvious, however, that the if these two parameters are similar in magnitude the fraction of occupied patches can be expected to be very small, even if the rate of dispersal of propagules from occupied patches is very high. Levins also investigated the influence of temporal variation in extinction and colonization rates on the size and probability of persistence of species subdivided into local populations.

The above model is clearly too simplistic to be of much value in the management of real populations. Many subsequent authors (see review by Hanski 1991) have replaced Levins' simple assumptions with more biologically realistic representations of both the dispersal of organisms between habitat patches and of the local dynamics of populations within patches. However, the fundamental processes and variables of interest, i.e., dispersal,

extinction, percent occupancy of available habitat, and metapopulation persistence, have not changed.

Most early work involving metapopulation models was concerned with insect populations, either with understanding the reasons for persistence of insect species subject to wide fluctuations in local population abundance (den Boer 1968) or with designing control strategies to reduce the frequency of widespread pest outbreaks (Levins 1969). In the 1980s conservation biologists turned to metapopulation theory as a means of designing preservation strategies for vertebrate species that, although once widespread, were becoming restricted to isolated subpopulations because of increasing habitat fragmentation. The early models were extended to include influences of local population size (Hanski 1985), local population structure (Lande 1987) and spatial dispersal patterns (Ray and Gilpin. 1991). The theory has also been extended to include predator-prey and host-parasitoid dynamics (Murdoch et al. 1985, Sabelis et al. 1991).

The relevance of this work to pesticide risk assessment comes from the observations that many wildlife species of management interest are, effectively, metapopulations. Their distribution patterns have been changed by decades of habitat conversion as the original forests and prairies of North America have been transformed into a mosaic of agricultural, urban/suburban, and successional landscapes. Pesticides of equal toxicity will have differential impacts on wildlife species depending on patterns of habitat utilization, degree of population isolation, dispersal ability, and other aspects of population biology included in metapopulation models.

Lande (1987) formulated a model of extinction and persistence in territorial populations that is a direct descendent of Levins' (1969) original model. Subsequently, other authors have developed much more detailed models of the Northern Spotted Owl, intended for use in predicting the influence of specific habitat management regimes on the recovery of this endangered subspecies. Lamberson et al. (1992) described a metapopulation model of the Northern Spotted Owl (*Strix occidentalis caurina*). In their model habitat patches are defined as nesting territories and local populations are defined as nesting pairs. A nesting pair annually produces young according to either a fixed fecundity rate or a randomly varying

fecundity rate. The juvenile birds disperse at the end of each breeding season, with juvenile males seeking an unoccupied nesting territory and juvenile females seeking a site occupied by a solitary male. The probability that a dispersing juvenile finds a suitable site before it dies is determined by the fraction the total landscape that consists of suitable sites, the fraction of those sites that is already occupied by nesting pairs, and the number of sites a juvenile can search before it dies. Adult birds are subjected to annual mortality, and nesting sites are subjected to disturbance through timber harvesting. adults nesting on a harvested site must disperse and locate new, unoccupied sites. The outputs from the model, which are updated on an annual time-step, include the total number of suitable nesting sites, the number of sites that are occupied by nesting pairs, and the number of sites occupied by single males.

Lamberson et al. (1992) used the model to evaluate the influence of initial population size, the proportion of the landscape suitable for occupancy by spotted owls, and the degree of interannual variability in fecundity (reflecting variability in food supply). Several interesting effects were found. First, because the sexes were modeled separately and colonization of a suitable site by both a male *and* a female s required to establish a nesting pair, the entire metapopulation invariably declined to extinction if the number of nesting pairs fell below a threshold determined by the searching abilities of the dispersing juveniles and the proportion of suitable habitat. This well-known phenomenon is termed by population biologists the "Allee effect" after the biologist who first described it. Second, Lamberson et al. (1992) investigated the influence of habitat availability on the probability of survival of the metapopulation under conditions of no, low, and high environmental variability. They found that, for the case of no environmental variability, extinction always occurred if less than a fixed percentage of the landscape (determined by dispersal ability) was suitable, and that extinction never occurred if the percentage of suitable habitat was greater than the threshold. Environmental variability had the effect of smoothing the transition from inevitable extinction to indefinite persistence, so that there was a small probability of persistence for habitat suitabilities slightly below the deterministic threshold and a small probability of extinction for suitabilities somewhat higher than the threshold.

By examining a range of parameter values consistent with the current state of knowledge of spotted owl population biology, the authors found that the effective persistence threshold for the metapopulation lies somewhere between 10% and 25% suitability of available habitat. Lamberson et al. (1992) also simulated a potential future timber harvesting regime in which the availability of nesting habitat was reduced gradually for 20 years and then stabilized at a level of 20%. They found that, although the simulated owl metapopulation eventually stabilized, there was significant time lag during which the total population of adult owls and the per cent occupancy of suitable sites was relatively constant. The implication of this result, according to the authors, is that it would be relatively difficult to use population monitoring data collected during the harvest period to determine the ultimate response of the owl metapopulation to habitat reduction.

Lamberson et al. (1994) used a different metapopulation model to evaluate the influence of patch size and spacing on the viability of the Northern Spotted Owl. The landscape was portrayed as a rectangular array of identical circular clusters containing potential owl habitat. Each cluster consisted of a collection of territories, some or all of which were assumed to be suitable as nesting sites. All of the space between clusters was assumed to be unsuitable habitat. This idealized landscape was intended to approximate the real landscape inhabited by spotted owls, which consists of patches of old-growth forest of with differing abilities to support spotted owls separated by areas of cut forest. Within each site, owl reproduction, survival, and dispersal were modeled in the same way as Lamberson et al. (1992), except that only females were considered. Dispersal was assumed to be successful if a juvenile female found an unoccupied but suitable territory within a specified number of searches.

Dispersal within clusters was simulated using a "random walk": starting from the territory of birth, a dispersing juvenile female was assumed to have an equal probability of searching any adjacent territory. If that territory was suitable and unoccupied, it became occupied by the dispersing bird. Otherwise, the bird moved, again in a random direction, to another adjacent territory. After a fixed number of unsuccessful searches, the dispersing juvenile was assumed to exit the cluster in a random direction. Two sources of mortality

were imposed on juvenile females dispersing between clusters: first, a juvenile was assumed to die if a straight line in the selected direction did not intersect another cluster. If a line in the selected direction did intersect a cluster, then the probability of survival during transit between the clusters was assumed to decline exponentially with the distance between clusters. A female successfully arriving at a new cluster searched it in the same way as her natal cluster and continued to search until she either died during transit, found an unoccupied suitable territory, or searched a total of 22 sites. All birds that searched 22 sites without success were assumed to die.

Landscape parameters investigated by the authors included the percentage of the total landscape included within habitat clusters, the number of sites within each cluster, the percentage of sites within each cluster suitable for nesting, the fraction of sites within a cluster searched prior to exiting, and the rate of mortality during dispersal. The authors evaluated the influence of different reserve design patterns on the mean occupancy of nesting sites, defined as the fraction of suitable sites occupied by nesting females.

According to the authors, field studies suggest that approximately 60% of the forested area within the range of the Northern Spotted Owl provides suitable nesting habitat. Assuming that 60% of the sites within each cluster are suitable and that a maximum of 22 sites can be searched by dispersing juveniles, simulated spotted owl metapopulations did not achieve a stable mean occupancy unless the average cluster contained at least 15 sites. Using a mean suitability of 80%, a stable population could be achieved at a smaller mean cluster size but mean occupancy declined rapidly at cluster sizes below 10 sites per cluster. For any fixed total reserve size and percent suitability, the equilibrium mean occupancy was found to increase with the size of the clusters. Lamberson et al. (1994) also investigated the influence of (1) the fraction of the total landscape occupied by clusters and (2) the distance between clusters on mean occupancy. They found that for small cluster sizes (i.e., 10 or fewer sites per cluster) increasing the fraction of the landscape in clusters and decreasing the distance between clusters both significantly increased mean occupancy; for cluster sizes greater than 25 there was little effect.

The authors used their results to evaluate the adequacy of the reserve design proposed for the Northern Spotted Owl. They concluded that, in general, the proposed sizes and spatial distributions of proposed "Habitat Conservation Areas" is adequate, provided that the recovery of currently degraded habitat within the HCAs is rapid.

Lindenmayer and Lacy (1995a, b) used the multipopulation version of VORTEX (Section 2.2) to evaluate the metapopulation stability (expressed as probability of persistence in the metapopulation as a whole and the inter-annual variability in abundance of local populations) of Leadbeater's Possum (*Gymnobelidius leadbeateri*) in fragmented Australian old-growth forests. Effects of patch size and number on stability were simulated by varying the carrying capacities and number of local populations; no attempt was made to simulate the influence of inter-patch distance or spatial distribution. The authors found, like Lamberson et al., that increasing the size of patches enhanced the stability of the metapopulation as a whole. When all patch sizes were small, metapopulation extinction rates were invariably high and emigration actually *decreased* metapopulation stability.

Lande's (1987) and Lindenmayer and Lacy's (1995a, b) models are more obviously relevant to pesticide risk assessment problems than is the more species-specific model of Lamberson et al. Neither, however, may provide sufficient biological realism to support pesticide regulation. In particular, neither provides for explicit consideration of local habitat requirements and distributions within agricultural landscapes. By following the example of Lamberson et al. (1992, 1994) population biologists could develop models specifically tailored to species and exposure regimes of interest in pesticide regulation. Such models could provide useful information for risk assessment if (1) the species of interest is, because of its intrinsic biological requirements or because of habitat fragmentation caused by habitat change, restricted to relatively isolated subpopulations between which dispersal and recolonization occur, (2) pesticide applications have the potential to increase the risk of extinction of local populations, and (3) it is the persistence of the species as a whole, not the persistence of individual local populations, that is the regulatory endpoint of interest.

2.4 Spatially-Explicit Models

Spatially-explicit models may be thought of as extensions of individual-based or metapopulation models in which the organisms or subpopulations are distributed over a realistic rather than an idealized landscape (Dunning et al. 1995). "Suitable" and "unsuitable" habitat types can defined explicitly in terms of vegetation, topography, or soil type. Temporal changes in habitat suitability can readily be simulated. For management applications, spatially-explicit models can utilize landscape maps derived from aerial surveys and remote sensing. For obvious reasons, growth of research and application of these models did not really begin until the late 1980s and the majority of the research performed using this approach has been published within the last five years.

The approach appears especially suited to the study of mobile animal populations that forage and disperse over large, heterogeneous areas. The spatially-explicit approach permits ecologists to integrate theory and observation on foraging behavior and reproduction in individual animals, relate these to specific measurable habitat characteristics, and infer influences of habitat change on populations. As noted by Pulliam (1994), information on environmental contaminant distributions and effects can easily be integrated into the same framework. Because spatially-explicit models often deal with individuals, the full array of individual physiological characteristics can also be incorporated. Such models can be thought of simply as individual-based models in which the location and directional movement of the organism are included as additional characteristics.

The most thoroughly explored and tested models of this type have been developed for populations of ungulates foraging in Yellowstone National Park (Turner et al. 1993, 1994) and for the population of Bachmann's Sparrow nesting on the U.S. Department of Energy Savannah River Site (Pulliam et al. 1992). Turner et al. (1993) simulated the influence of landscape heterogeneity on winter grazing in "generic" ungulates. A standard energetics model was used to simulate the daily foraging intake and energy balance of an animal as a function of body weight, forage availability, and activity level. The authors then investigated the influence of different ungulate movement "rules" and patterns of forage availability on the energy balance and survival of model populations. Landscapes in which resource patches

(sagebrush-grassland communities) were randomly distributed across the landscape were compared with landscapes derived directly from vegetation maps for Yellowstone. During each time step of the simulation, an animal feeds on resources within the patch it occupies. It may move to another patch; the probability of movement increases as it feeds and depletes the forage at its current location. While an animal is moving between patches it cannot feed.

Results obtained from the model generally supported previous theoretical predictions that (1) when resources are abundant, landscape pattern and movement rules should have no influence on weight maintenance and survival, (2) when resources are scarce, aggregated resources (i.e., the real Yellowstone landscape) should support more animals than randomly dispersed resources, and (3) when resources are scarce, behavioral rules that allow the animals to discern resource abundance at distant sites or to move over greater distances should improve survival.

Turner et al. (1994) extended their original model and used it to explore the effects of fire on free-ranging elk (*Cervus elaphus*) and bison (*Bison bison*) populations in northern Yellowstone Park. In the new analysis, the authors derived a six-category habitat map from GIS data maintained by the National Park Service and assigned to each category a winter forage abundance derived from actual field measurements (available separately for unburned sites and for sites burned during the 1988 fires). The foraging rule used assumed that each animal visually searches within a circle around its current location and moves to the site with the highest quality; it may continue searching and moving until it either obtains its maximum daily intake or reaches its maximum daily movement distance. Because snow conditions are an important determinant of winter ungulate survival, snow was simulated in the model. A snow subroutine assigned monthly snow depth values to each grid cell based on observed data and on known influences of topography on snow depth. Foraging behavior and energetic costs were both assumed to be affected by snow depth.

The authors were able to calibrate and test their model using observed data collected both before and after the 1988 fire. For all three years, data were available on winter precipitation, fall elk/bison count, and overwintering elk/bison survival. After model parameters were calibrated so that overwintering survival during these three years matched

the available data, simulation experiments were performed to evaluate the influence of winter severity, fire size, and fire pattern on ungulate survival. Observed snowfall during the most severe and most mild winters recorded in this century at Yellowstone were used to evaluate the influence of winter severity. Three levels of fire severity, expressed as the percentage of the study area burned, were examined. A range of alternative fire patterns was evaluated: a fragmented burn was simulated by distributing burned grid cells at random over the whole map; a clumped burn was simulated by generating a single patch of burned cells centered on an arbitrary location. Several intermediate patch distributions were also evaluated, including the actual observed burn distribution of the 1988 fire. In all, 24 different scenarios were evaluated.

The authors found that winter snow was the most important determinant of ungulate survival. Fire severity and pattern influenced survival only during average and severe winters. Provided winters were mild or average, large fires actually produced better long-term survival than small fires due to their stimulating effect on forage availability during post-fire winters. For small to moderate fires, ungulate survival was greater with clumped than fragmented fire patterns. The authors concluded that fires and spatial fire patterns have an important influence on ungulate population dynamics in Yellowstone only if severe winter conditions occur in the post-fire winter.

Pulliam et al. (1992) described a generalized spatially-explicit population model for bird dispersal, applied to the Bachmann's sparrow (*Aimophila aestivalis*). The objective of the model was to describe influences of spatial variation in habitat suitability on the abundance and persistence of sparrow populations in a managed pine plantation. The model as described in the original paper is closely similar to the spotted owl model of Lamberson et al. (1994), discussed above. Only female birds are included, and the only life-history characteristics simulated is dispersal. The principal differences between the models are in descriptions attached to the grid cells. In the model of Pulliam et al., grid cells are identified with pine stands of different ages. Bachman's sparrows nest only in young (5 years old or less) or mature (>80 years old) pine stands. The simulated plantation consists of a number of tracts of different ages. As the simulation proceeds, newly-seeded tracts become suitable

nesting sites and previously suitable tracts age and become unsuitable. Trees are harvested on a 21-year rotation, except for a certain number of tracts of mature pine forest that provided a stable source of dispersing birds. The authors evaluated the influence of different model parameters on the abundance and persistence of populations simulated for 100 years (five rotations). They found that parameters relating to mortality and reproduction were more important than those relating to dispersal (site selectivity, dispersal mortality). Population size increased linearly with the number of tracts left in mature forest, but mature forest was not required to maintain viable sparrow populations.

Liu (1993) extended the BACHMAP model in two significant ways. First, he modified it to accept landscape classification information from a GIS. Second, he developed an economics subroutine that calculates growth, yield, income, cost, and net-present-value estimates for each tract. The extended model is coded in an object-oriented programming language, so that it is modular and can easily be adapted to different species or landscape types. Results of actual management applications are not yet published, as of the date of preparation of this report.

Other recently-published spatially-explicit models simulate physiology as well as behavior. Loza et al. (1992) described a model of cattle grazing on open rangeland that simulates the influence of physiological status (energy and water balance) on the grazing behavior and land use of grazing animals. Jager et al. (1993) described a spatially-explicit version of the smallmouth bass model of DeAngelis et al. (1991) that simulates reproduction, foraging, and growth in a riverine population of smallmouth bass.

The principal advantages of spatially-explicit models include flexibility and realism, especially realism with respect to spatial representation of the environment. Virtually any physical or biological process can be included in such models, provided a model of that process can be developed. Both short-term and long-term events can be simulated. Extremely detailed representations of the landscape, including direct interfacing with GIS systems, is possible. The principal disadvantages are complexity of some of the models (a disadvantage if there are no data) and, especially, the relative immaturity of the applications. The vast majority of the published models are very recent. Few applications utilizing GIS

technology have yet been published, although several are currently being developed. Given the flexibility of the approach, specific applications for pesticides should be straightforward: specify the spatial scale (local or regional), the species and landscape types of interest, and the pesticide application scenarios. The object-oriented programming approach described by Liu (1993) appears to provide an important advance in modeling technique because it permits a generalized model structure to be specifically tailored to a variety of risk assessment scenarios.
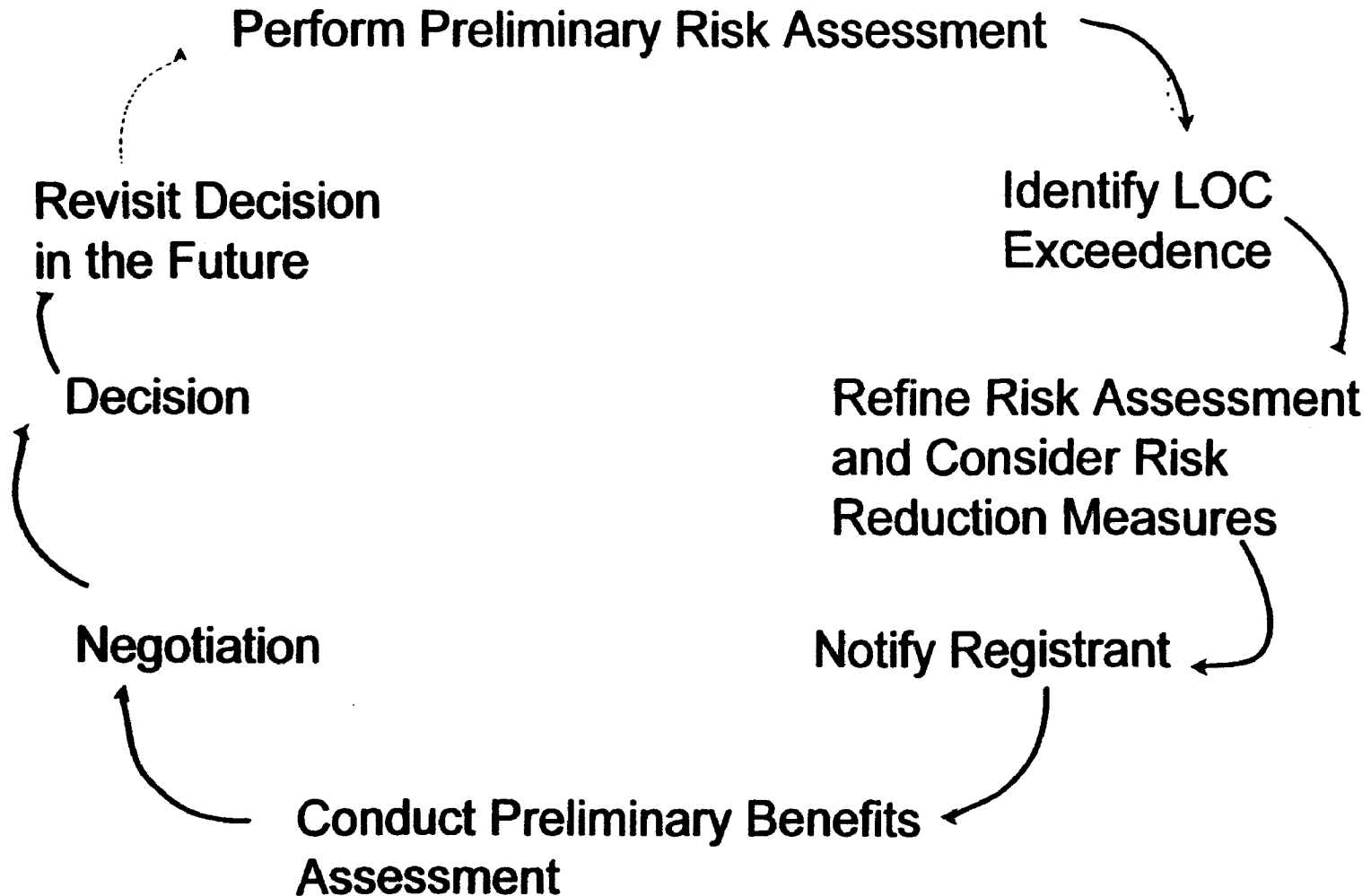
3.0 INTEGRATION OF ECOLOGICAL MODELS INTO THE NEW PARADIGM

Figure 1 presents a schematic version of the implementation process for the New Paradigm (Avian Effects Dialogue Group 1994). According to this scheme, if the initial screening of a pesticide shows potential exceedence of Levels of Concern, then a "refined risk assessment" may be performed. The Avian Effects Dialogue Group identified fourteen specific kinds of information that could contribute to these refined risk assessments. The modeling approaches discussed in this report could contribute to these refined assessments by (1) allowing effects to be expressed in terms of population abundance and persistence rather than as fractions of an LC_{50} or other laboratory test endpoint, (2) integrating information on lethal and sublethal effects (including behavioral effects), and (3) accounting for spatiotemporal variations in exposure.

The Avian Effects Dialogue Group discussed simulation modeling as a potential approach to risk characterization, but provided no specific recommendations. This review demonstrates that progress in some types of ecological modeling has been significant in recent years. All four types of models discussed in this report could be used to implement the New Paradigm.

Viewed within the Framework for Ecological Risk Assessment (U.S. Environmental Protection Agency. 1992), all of these models are risk characterization techniques: they express effects of pesticides or other stressors in terms that are understandable to decision makers and are compatible with cost-benefit analyses or other management-related evaluations.

Figure 1. Implementation Process for the New Paradigm

Perform Preliminary Risk Assessment

Identify LOC Exceedence

Revisit Decision in the Future

Refine Risk Assessment and Consider Risk Reduction Measures

Decision

Negotiation

Notify Registrant

Conduct Preliminary Benefits Assessment

3.1 Types of Model Applications

There are at least three possible uses of models within the New Paradigm:

Initial registration

Initial pesticide registration is a predictive activity involving the estimation of potential changes in population size or reproductive success from standard toxicity test data. Applications of age-structured models to predictive assessment problems are described by Barnthouse et al. (1990), Emlen (1990), and Barnthouse (1993). Inter-species and inter-life stage extrapolation methods described by Barnthouse et al. (1990) can be used to quantify prediction uncertainty and express risks in terms of ranges of potential effects associated with a given exposure or ranges of exposure associated with a given effects levels. As suggested by Emlen and Pikitch (1989), a few generic population models can be made to represent major life-history types of organisms, especially vertebrates (mouse, moose, sparrow, eagle). Such models could be used to illustrate the consequences of contaminant exposure for populations of organisms having different life-history characteristics.

Because of the inherent limitations of age/stage-structured models, the above approach cannot accommodate spatial or temporal variations in exposure and thus cannot be used to evaluate the influence of application regimes or site-specific environmental variability on the effects of pesticides. Such information may, however, not be needed for initial decision making. If predicted effects using conservative exposure scenarios are shown to be inconsequential, then no additional analyses may be necessary.

Another way to introduce population-level phenomena into initial registration decisions would be to expand the concept of of reference environments, as it is already used in exposure assessment, to include reference populations. Descriptions of a reference field could include, in addition to estimates of soil type, slope, rainfall, and other physical parameters used in pesticide fate models, estimates of the seasonal distribution and foraging characteristics of a reference ground-feeding bird. An individual-based model would use this information to assess the impact of pesticide application on a reference bird population. Besides permitting detailed evaluation of alternative application patterns, this approach

would facilitate assessments of pesticides with high potential toxicity but low environmental persistence.

Special Review

Substantial quantities of field data are often available for pesticides undergoing special reviews. For these cases, site-specific population models may aid in interpreting the results of field studies. In the case of granular carbofuran (Houseknecht 1993), for example, information on acute mortality of birds due to carbofuran exposure was available both from incidental observations and from field experiments. The value of these data for risk assessment was limited, however, because pesticide effects could only be quantified in terms of numbers of dead birds. An individual-based model of a foraging bird population, developed using the approach described by Pulliam (1994), could have been used to estimate the distributions of exposures within a local population of birds, the fraction of those birds likely to have received a lethal dose of carbofuran, and the long-term consequences of continued carbofuran application for the abundance and persistence of a reference population. Such model applications are especially feasible for birds because of the well-developed state of avian foraging theory and the relative ease of validating species-specific avian foraging models (Pulliam 1994).

Regional assessment

There is increasing interest within the EPA in performing regional, or "place-based" assessments that integrate a variety of kinds of environmental hazards and can be used to prioritize regulatory activities for specific watersheds or regions. For example, pesticide use patterns and ecosystem types present in the Midwest corn belt differ substantially from those present in the Gulf Coast region. If the ecological importance of these differences could be incorporated in risk assessments, then region-specific restrictions or labeling requirements could be designed. Issues that could be addressed might include the cumulative impacts of runoff from a region within which large quantities of a few pesticides are used, or impacts on wide-ranging species that forage over a mosaic of landscape types. For these applications,

depending on scale, spatially-explicit models or metapopulation models would be appropriate. Such models can accommodate land classification data that are already available from many sources. Turner et al. (1995) And Liu et al. (In press) have already shown that such applications are technically feasible.

Table 1 summarizes the types of models appropriate for each of the above applications. For initial registration decisions, little or no site or region-specific information is likely to be available. Relatively little toxicity data may be available as well. Thus, the models with the fewest information requirements, i.e., age/stage-based models, are the most likely to be useful. Provided that (1) reference population descriptions have been developed, and (2) some information about physiology or time-dependent pesticide fate patterns is available, then individual-based models could enable consideration of more complex phenomena. The same types of models may be used for special reviews. However, for a special review more information is likely to be available, and spatial patterns of use may have been established. If local or regional extinctions are identified as an ecological issue of concern, then metapopulation models may be useful. For regional assessments, it is likely that spatiotemporal pesticide use patterns and explicit characteristics of the landscape will be relevant. Models that cannot accommodate space, i.e., age/stage-based models and individual-based models, will not be able to address the relevant questions. Metapopulation models, and, especially, spatially-explicit models, would appear to be the best choices in principle.

Table 1. Modeling approaches suitable for three types of pesticide risk assessment applications

Applications	Models			
	age/stage based	individual-based	meta-population	spatially explicit
Initial Registration	X	X		
Special Review	X	X	X	
Regional assessment			X	X

3.2 State-of-Development of Modeling Approaches

Table 2 compares the four modeling approaches discussed in this report with respect to the evaluation criteria discussed in section 1.2. All four approaches are highly flexible in form and can represent a wide range of populations of interest. Less data would in general be required to implement age/stage-structured models than to implement the other model types, however, as noted in section 2, all four approaches can encompass a range of complexity so that complexity *per se* is not a useful evaluation criterion.

Table 2. Comparative evaluation of modeling approaches.

Models

Criteria	age/stage-based	individual-based	meta-population	spatially explicit
Endpoints	H	H	H	H
Resolution	L	H	M	H
Generality	H	M	H	L
Acceptance	H	M	M	L

The four approaches differ significantly with respect to the other three evaluation criteria. Age/stage-structured models are, according to the definitions used in this report, spatially homogeneous (spatially-structured variants of this model type would be classified as metapopulation models). As normally applied, age/structured models are used to characterize the long-term or steady-state behavior of populations and cannot directly address phenomena (e.g., transient pulses of contaminant exposure) that are short with respect to the lifetime of a single organism. Individual-based models and spatially explicit models, in contrast, have arbitrarily high degrees of resolution. The activities of individual organisms can be simulated on any time-scale; the size of cells in spatially-distributed models can be made arbitrarily

large or small. In both cases the resolution of the available data and the needs of the assessment are the limiting factors. Metapopulation models are intermediate in resolution: space can be at least implicitly represented in terms of immigration/emigration/extinction processes. Like age/stage-structured models, however, metapopulation models are generally best suited to addressing effects of long-term exposures.

As noted by Levins (1966), a tradeoff can usually be expected between generality and spatiotemporal resolution in models. Age/stage-structured models have been developed for virtually every type of living organism. The versatility of the metapopulation approach, at least when applied to vertebrates, is demonstrated by the number of species for which the multipopulation version of the VORTEX model has been implemented. In contrast, physiologically and behaviorally-oriented individual-based models such as those of DeAngelis et al. (1991) and Pulliam et al. (1992) are highly specific. The underlying theories of foraging, bioenergetics, and reproduction are quite general, however, the number of species-specific parameters needed to implement an individual-based model can be quite large. Spatially-explicit models require, in addition, site-specific data on landcover, weather, and other environmental influences on the activities of the organisms being modeled.

With respect to degree of acceptance by the scientific community, age/stage-based models are by far the best-developed type discussed in this report. They are the type most people immediately think of when they hear the term 'population model". The basic Leslie matrix and its variants are the backbone of quantitative fisheries assessment, with literally hundreds of applications over 50 years. User-friendly modeling software is widely available. The more general stage-based models have been less-widely used in management, although they are common in plant demography and applied entomology.

Metapopulation models have a much shorter history, but have become very widely used in conservation biology over the last decade. The more complex models, such as the multipopulation version of VORTEX, provide a useful extension of age/stage-based models for situations in which differential exposures to isolated subpopulations are important. This will often be the case for rare or endangered species, which are restricted to specific habitat types. Like age/stage-structured models, they can be relatively general and applicable to a

variety of different life-history types, as has been shown by the ease with which the VORTEX model has been adapted to a variety of mammalian species.

Despite its formulation in terms of individual organisms, VORTEX is in principle equivalent to a classical age/stage-structured model. Caswell and John (1992) showed that all matrix-type population models can be derived from models of the birth, reproduction, and death processes of individual organisms; for large population sizes VORTEX and its matrix equivalent would provide identical results. Models that incorporate physiological or behavioral influences on individuals, or that involve explicit simulation of interactions between organisms and their surrounding landscape, are fundamentally distinct from any previous approach to population modeling. Such represent the future rather than the present of population biology. The majority of published accounts of these kinds of models have appeared in the peer-reviewed literature only within the past three years. No standardized modeling software is available to support their development. Only a few experts, primarily associated with the authors of the papers cited in this report, have had any significant experience in developing and applying these models. The object-oriented software described by Liu (1993) provides a general framework that would, if widely adopted, significantly simplify the programming aspect of model development. However, developing a sound biological content for the models will still be a major undertaking.

4.0 CONCLUSIONS AND RECOMMENDATIONS

1. The state-of-the-science in population biology is sufficient to support the development and use by EPA of models that express risks to aquatic and terrestrial biota from pesticide exposure in terms of population-level rather than individual-level endpoints.

2. Age/stage-structured models and metapopulation models can be used to qualitatively describe the influences of specific levels of mortality and reproduction on organisms with different life-history types and distributional patterns. These approaches to modeling are extensively documented in the scientific literature and are widely used in resource management. No further scientific development is needed to support use by EPA.

3. Individual-based models and spatially-explicit models can quantitatively describe effects of lethal and sublethal exposures to pesticides for specific target species in specific environments. These approaches are new and there have been few management applications. Implementation of these models requires substantial information concerning (1) the modes of action and environmental fate of the pesticides being assessed, and (2) the behavior, spatial distribution, and population dynamics of the species of interest.

4. Steps the Agency can take to implement these models include:

Broaden the management basis for decision making concerning pesticides. As documented by Troyer and Brody (1994), there are no consistent ecological assessment endpoints within EPA. Visible kills of birds and evidence of toxicity in the laboratory, have been used as a basis for decision making but predicted or observed effects on populations have not been. Specific population-level assessment endpoints and characteristic assessment scales, consistent with the types of decisions made at each stage of the pesticide assessment cycle (Figure 1), should be established.

Develop reference population data sets - Data sets should be developed for representative species and local environments that can be used in the same way as the "reference environments" used in pesticide fate modeling. These can then be used to parameterize age/stage based and individual-based models. The wildlife exposure handbook recently developed by EPA wildlife can serve as a good model.

Demonstrate models through actual applications. Application to a high-profile assessment problem is the best way to demonstrate the value of any assessment methodology. The ideal candidate studies would be special reviews or other assessments expected to involve sensitive ecological resources and high-value pesticides. Such assessments might be expected to take several years to complete and to justify significant expenditures of funds for laboratory and field data. The availability of time and data would, in turn, allow the development of credible models.

Fund research - Individual-based models and spatially-explicit models in particular lack a solid scientific foundation and, perhaps even more important, lack a corps of experienced practitioners. The best way to increase both the quality of the science and the number of practitioners is to fund research. Support of graduate and postgraduate fellowships in particular would be a highly cost-effective approach.

Train agency staff - Agency technical staff will not use a new methodology if they are unfamiliar with it and are not confident that it will improve their work. Training classes, and hands-on experience will be necessary. If the agency funds extramural scientists to develop any of the model types described in this report, then the contracts should require the model developers to work with EPA staff during the initial phases of implementation by the agency.

5.0 REFERENCES

Andrewartha, H.G., and L. C. Birch. 1954. *The Distribution and Abundance of Animals.* University of Chicago Press, Chicago, Illinois.

Avian Effects Dialogue Group. 1994. *Assessing Pesticide Impacts on Birds.* RESOLVE, Inc., 1250 24th St. N.W. Washington, D.C. 20037.

Barnthouse, L.W., R. V. O'Neill, S. M. Bartell, and G. W. Suter II. 1986. Population and ecosystem theory in ecological risk assessment. pp. 82-96 IN: T.M. Poston and R. Purdy (eds.), *Aquatic Toxicology and Environmental Fate: Ninth Volume,* ASTM STP 921, American Society for Testing and Materials, Philadelphia, Pennsylvania.

Barnthouse, L. W. 1992. The Role of Models in Ecological Risk Assessment: A 1990's Perspective. *Environmental Toxicology and Chemistry* 11:1751-1760.

Barnthouse, L.W. 1993. Population-level effects. Pp. 247-274 IN: G. W. Suter II (ed.) *Ecological Risk Assessment.* Lewis Publishers, Chelsea, Michigan.

Barnthouse, L.W., G. W. Suter, II, and A. E. Rosen. 1990. Risks of Toxic Contaminants to Exploited Fish Population: Influence of Life History, Data Uncertainty, and Exploitation Intensity. *Environmental Toxicology and Chemistry* 9:297-311.

Beyer, J. E., and G. C. Laurence. 1980. A stochastic model of larval fish growth. *Ecological Modelling* 8:109-132

Caswell, H. 1989. *Matrix Population Models: Construction, Analysis, and Interpretation.* Sinauer, Inc., Sunderland, Massachussetts. 328 pp.

Caswell, H., and A. M. John. 1992. From the individual to the population in demographic models. Pp. 36-61 IN: D. L. DeAngelis and L. J. Gross (eds.) *Individual-Based Models and Approaches in Ecology.* Chapman and Hall, New York.

Dale., V. I., and R. H. Gardner 1987. Assessing regional impacts of growth declines using a forest succession model. *Journal of Environmental Management* 24:83-93.

DeAngelis, D. L. L. Godbout, and B. J. Shuter. 1991. An individual-based approach to predicting density-dependent compensation in smallmouth bass populations. *Ecological Modelling* 57: 91-115.

denBoer, P.J., 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica* 18:165-194.

deKroon, H., A. Plaisier, J. Van Groenendael, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67:1427-1431.

Dunning, J. B., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* 5: 3-11.

Emlen, J. M. 1989. Terrestrial population models for ecological risk assessment: a state-of-the-art review. *Environmental Toxicology and Chemistry* 8:831-842.

Emlen, J. M., and E. K. Pikitch. 1989. Animal Population Dynamics: Identification of Critical Components. *Ecological Modeling.* 44:253-273.

Ferson, S. 1990. RAMAS/Stage. Generalized stage-based modeling for population dynamics. Applied Biomathematics, Setauket, New York.

Ferson, S., and H. R. Akcakaya. 1989. RAMAS/Age user manual. Modeling fluctuations in age-structured populations. Applied Biomathematics, Setauket, New York.

Foose, T. J., R. C. Lacy, R. Brett, and U. S. Seal. 1992. Kenya black rhinoceros population and habitat viability assessment. International Union for the Conservation of Nature and Natural Resources, Captive Breeding Specialist Group, Apple Valley, Minnesota.

Gurney, W. S. C., E. McCauley, R. M. Nisbet, and W. W. Murdoch. 1990. The physiological ecology of *Daphnia*: a dynamic model of growth and reproduction. *Ecology* 71:703-715

Hallam, T. G.,R. R. Lassiter, J. Li, and W. McKinney. 1990. Toxicant-induced mortality in models of Daphnia populations. *Environmental Toxicology and Chemistry* 9: 597-621.

Hanski, I. 1985. Single-species spatial dynamics may contribute to long-term rarity and commonness. *Ecology* 66:335-343.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnaean Society* 42:17-38.

Hanski, I. and M. Gilpin. 1991. Metapopulation dynamics: a brief history and conceptual domain. *Biological Journal of the Linnaean Society* 42:3-16.

Houseknecht, C. R. 1993. Ecological risk assessment case study: Special review of the granular formulations of carbofuran based on adverse effects on birds. Section 3 IN U.S. Environmental Protection Agency, A review of ecological assessment case studies from a risk assessment perspective. EPA/630/R-92/005, U.S. Environmental Protection Agency, Washington, D.C.

Huston, M. A., and T. M. Smith. 1987. Plant succession: life history and competition. *American Naturalist* 130:168-198.

Jager, H. I., D. L. DeAngelis, M. J. Sale, W. Van Winkle, D. D. Schmoyer, M. J. Sabo, D. J. Orth, and J. A. Lukas. 1993. An individual-based model for smallmouth bass reproduction and young-of-year dynamics in streams. *Rivers* 4:91-113.

Kooijman, S. A. L. M., and J. A. J. Metz. 1984. On thy dynamics of chemically stressed populations: the deduction of population consequences from effects on individuals. *Ecotoxicology and Environmental Safety* 8:254-274.

Lacy, R. C., and T. W. Clark. 1990. Population viability assessment of the eastern barred bandicoot in Victoria. Pp. 131-146 IN: T. W. Clark and J. H. Seebeck, (eds.) *The management and conservation of small populations.* Chicago Zoological Society, Brookfield, Illinois.

Lacy, R. C. 1993. VORTEX: a computer simulation model for use in population viability analysis. *Wildlife Research* 20:45-65.

Lacy, R. C., N. R. Flesness, and U. S. Seal. 1989. Puerto Rican parrot population viability analysis. International Union for the Conservation of Nature and Natural Resources, Species Survival Commission, Captive Breeding Specialist Group, Apple Valley, Minnesota.

Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. 1992. The effects of varying dispersal capabilities on the population dynamics of the northern spotted owl. *Conservation Biology.* 6:505-512.

Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. ,1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the northern spotted owl. *Conservation Biology.* 8:185-195.

Lande, R. 1987. Extinction thresholds in demographic models of terrestrial populations. *American Naturalist* 130:624-635.

Lassiter, R. R. and T.G. Hallam. 1990. Survival of the fattest: implications for acute effects of lipophilic chemicals on aquatic populations. *Environmental Toxicology and Chemistry*. 9:585-596.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33:183-212.

Levins, R. 1966. The strategy of model building in population biology. *American Scientist* 54:421-431.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237-240.

Lindenmayer, D. B., T. W. Clark, R. C. Lacy, and V. C., Thomas. 1993. Population Viability Analysis as a tool in wildlife management: a review with reference to Australia. *Environmental Management* 17:745-758.

Lindenmayer, D. B., and R. C. Lacy. 1995a. Metapopulation viability of Leadbeater's possum, *Gymnobelideus leadbeateri*, in fragmented old-growth forests. *Ecological Applications* 5:164-182.

Lindenmayer, D. B. and R. C. Lacy. 1995b. Metapopulation viability of arboreal marsupials in fragmented old-growth forests: comparison among species. *Ecological Applications*. 5:183-199.

Liu, J. 1993. An introduction to ECOLECON: a spatially-explicit model for ECOLogical ECONomics of species conservation in complex forest landscapes. *Ecological Modelling* 70:63-87.

Liu, J., J. B. Dunning, and H. R. Pulliam. Assessing alternative management strategies: an example coupling GIS with spatially-explicit models. *Conservation Biology* (in press)

Loza, H. J., W. E. Grant ,J. W. Stuth, and T. D. A. Forbes. 1992. Physiologically based landscape use model for large herbivores. *Ecological Modeling* 61:227-252

MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.

Madenjian, C. P., and S. R. Carpenter. 1991. Individual-based model for growth of young-of-the-year walleye: a piece of the recruitment puzzle. *Ecological Applications* 1:268-278.

Maguire, L. A., R. C. Lacy, R. J. Begg, and T. W. Clark. 1990. An analysis of alternative strategies for recovering the eastern barred bandicoot. Pp. 147-164 IN: T. W. Clark and J. H. Seebeck (eds.) *The Management and Conservation of Small Populations*. Chicago Zoological Society, Brookfield, Illinois.

McCauley, E., W. W. Murdoch, R. M. Nisbet, and W. S. C. Gurney. 1990. The physiological ecology of *Daphnia*: a dynamic model of growth and reproduction. *Ecology* 71:716-732.

Meyer, J. S. and M. S. Boyce. Life historical consequences of pesticides and other insults to vital rates. pp. 349-363 IN: Kendall, R. J. and T. E. Lacher, Jr. (eds.) *Wildlife Toxicology and Population Modeling*, Lewis Publishers, Boca Raton, Florida.

Murdoch, W. W., J. Chessson, and P. Chesson. 1985. Biological control in theory and practice. *American Naturalist* 125:344-366.

Pulliam, H. R., J. B. Dunning, Jr., and J. Liu. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* 2:165-167.

Pulliam, H. R. 1994. Incorporating concepts from population and behavioral ecology into models of exposure to toxins and risk assessment. pp. 13-26 IN: Kendall, R. J. and T. E. Lacher, Jr. (eds.) *Wildlife Toxicology and Population Modeling*. Lewis Publishers, Boca Raton, Florida.

Ray, C., and M. E. Gilpin. 1991. The effect of conspecific attraction on metapopulation dynamics. *Biological Journal of the Linnaean Society* 42:123-134.

Rose, K. P., and J. H. Cowan Jr. 1993. Individual-based model of young-of-the-year striped bass population dynamics. I. Model description and baseline simulations. *Transactions of the American Fisheries Society* 122:415-438

Sabelis, M. W., O. Diekman, and V. A. A. Jansen. 1991. Metapopulation persistence despite local extinction: predator-prey patch models of the Lotka-Volterra type. *Biological Journal of the Linnaean Society* 42:267-283.

Samuels, W. B. and A. Ladino. 1983. Calculations of Seabird Population Recovery from Potential Oil spills in the Mid-Atlantic Region of the United States. *Ecological Modeling* 21:63-84.

Seal, U.S., and T. J. Foose. 1989. Javan rhinoceros population viability analysis and recommendations. International Union for the Conservation of Nature and Natural Resources, Captive Breeding Specialist Group, Apple Valley, Minnesota.

Seal, U. S., and R. C. Lacy. 1989. Florida panther population viability analysis. International Union for the Conservation of Nature and Natural Resources, Captive Breeding Specialist Group, Apple Valley, Minnesota.

Society of Environmental Toxicology and Chemistry (SETAC). 1994. Aquatic Dialogue Group: Pesticide risk assessment and mitigation. SETAC Press, 1010 North 12th Ave., Pensacola, Florida 32501.

Shugart, H. H. 1984. *A Theory of Forest Dynamics*. Springer-Verlag, New York.

Tipton, A. R., R. J. Kendall, J. F. Coyle, and P. F. Scanlon. 1980. A Model of the Impact of Methyl Parathion Spraying on a Quail Population. *Bulletin of Environmental Contamination and Toxicology* 25:586-593.

Troyer, M. E., and M. S. Brody. 1994. Managing ecological risks at EPA: Issues and recommendations for progress. EPA/600/R-94/183. U.S. Environmental Protection Agency, Washington, D.C.

Turner, M. G., Y. Wu, W. H. Romme, and L. L. Wallace. 1993. A landscape simulation model of winter foraging by large ungulates. *Ecological Modelling* 69:163-184.

Turner, M. G., Y. Wu, W. H. Romme, L. L. Wallace ,and A. Brenkert. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecological Applications* 4:472-496.

Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, J. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit population models in land management. *Ecological Applications* 5:12-16.

Urban, D. L., and N. J. Cook. 1986. Hazard Evaluation, Standard Evaluation Procedure, Ecological Risk Assessment. EPA-540/9-85-001. U.S. Environmental Protection Agency, Washington, D.C.

U.S. Environmental Protection Agency. 1992. Framework for Ecological Risk Assessment. EPA/630/R-92/001. U.S. Environmental Protection Agency, Washington, D.C.

van Groenendael, J., H. DeKroon, S. Kalisz, and S. Tuljapurkar. . 1994. Loop analysis: Evaluating life history pathways in population projection matrices. *Ecology* 75:2410-2415.

van Tienderen. P. H. 1995. Life cycle trade-offs in matrix population models. *Ecology* 76:2482-2489.

APPENDIX: ANNOTATED BIBLIOGRAPHY OF ECOLOGICAL MODELS

1.   Barnthouse, L. W. Population-level effects. IN: G. W. Suter, (ed.). *Ecological Risk Assessment*. Chelsea, Michigan: Lewis Publishers; 1993; pp. 247-274.
     Note: Overview of population modeling theory and applications, including case studies involving toxic chemicals.

2.   Barnthouse, L. W. The Role of Models in Ecological Risk Assessment: A 1990's Perspective. *Environmental Toxicology and Chemistry*. 1992; 11:1751-1760.
     Note: A review emphasizing (a) modeling approaches developed within the last decade; (b) applications to a broad array of environmental problems on local, regional, and global scales; and (c) the relevance of different types of models to different components of the risk assessment process.

3.   Barnthouse, L. W.; Suter, G. W.II, and Rosen, A. E. Risks of Toxic Contaminants to Exploited Fish Population: Influence of Life History, Data Uncertainty, and Exploitation Intensity. *Environmental Toxicology and Chemistry*. 1990; 9:297-311.
     Note: Analysis of risks of contaminants to fish populations performed by coupling standard toxicity test data to matrix-type population models derived from fisheries data. Risks related to chemical exposure compared to risks related to fishing and to environmental variability.

4.   Bartell, S. M.; O'Neill, R. V., and Gardner, R. H. Aquatic ecosystem models for risk assessment. *Analysis of Ecological Systems: State-of-the-Art in Ecological Modelling*. Lauenroth, W.K.; Skogerboe, G.V.; Flug, M. ed. Elsevier Scientific Publishing Company; 1983; pp. 123-127. (Developments in Environmental Modelling; v. 5).
     Note: Overview of Fate of Aromatics Model (Foam), originally developed by Bartell, and Standard Water-Column Model (SWACOM) originally developed by O'Neill. Both models derive from early aquatic ecosystem models developed for the International Biological Program in the early 1970s. Programming techniques and computer hardware have improved significantly since these models were first described, but the underlying ecosystem theory has changed very little.

5.   Baveco, J. M. and A. M. de Roos. Assessing the impact of pesticides on lumbricid populations: an individual-based modelling approach. *Jounral of Applied Ecology*. (submitted).
     Note: Physiologically-based model of earthworm population exposed to pesticides. Includes analytical results for steady-state and Monte Carlo analysis of stochastic responses.

6. Baveco, J. M. and R. Lingeman. An object-oriented tool for individual-oriented simulation: host-parasitoid system application. *Ecological Modelling*. 1992; 61:267-286.
   Note: Classical model of host-parasitoid interactions in a patchy environment, but illustrating use of object-oriented programming in a PC environment.

7. Belovsky, G. E. Modeling avian foraging: implications for assessing the ecological effects of pesticides. *Wildlife Toxicology and Population Modeling*, R. J. Kendall and T. E. Lacher, Jr. Boca Raton, FL: Lewis Publishers; 1994.
   Note: Presents a linear programming approach to optimal foraging (and consequent pesticide ingestion). Applied to cowbirds foraging on seeds and grasshoppers. Processes/factors modeled include foraging, ingestion, digestive constraints, energy requirements. Constraints consist of minimum daily energy intake, maximum digestive capacity, maximum foraging time. Addresses direct effects of pesticide on birds and indirect effects related to reduction in grasshopper abundance. Scenario analyses evaluated impact of reduced cowbird predation on effectiveness of pesticides at controlling grasshoppers.

8. Beyer, J. E. and G. C. Laurence. A stochastic model of larval fish growth. *Ecological Modelling*. 1980; 8:109-132.
   Note: Individual-based model of growth and survival of larval winter flounder.

9. Bird, S. L. Fate and exposure modeling in terrestrial ecosystems: a process approach. *Wildlife Toxicology and Population Modeling*, Kendall, R. J. and T. E. Lacher, Jr. Boca Raton, FL: Lewis Publishers; 1994; pp. 149-159.
   Note: Overview of PIRANHA modeling system developed by EPA Athens Lab. Consists of multimedia environmental fate models and supporting databases. Includes a drift model (FSCBG), a soil model (PRZM), a model of uptake in plants (no acronym), an of Craig Barber's FGETS model to uptake of contaminants by worms, and a pharmacokinetic model of contaminant uptake (ingestion pathway) by birds. Database information includes geographical distributions of soil thpe, crop production, and rainfall. No applications presented.

10. Bowers, M. A. Use of space and habitats by individuals and populations: dynamics and risk assessment. *Wildlife Toxicology and Population Modeling*, Kendall R. J. and T. E. Lacher Jr. Boca Raton, FL: Lewis Publishers; 1994.
   Note: Discusses importance of habitat selection as determinant of demographic "success." Source/sink populations, etc. no models, but some good references.

11. Brisbin, I. L. Jr. Application of a modified Richards sigmoid model to assess the uptake and effects of environmental contaminants upon birds. *Wildlife Toxicology and Population Modeling*, R. J. Kendall and T. E. Lacher, Jr. Boca Raton, FL: Lewis Publishers; 1994; pp. 161-170.
Note: Application of "Richards" 3-parameter model (an asymptotic sigmoid growth model that includes the von Bertalanffy, logistic, and Gompertz models as special cases) to contaminant uptake. Used to quantify change in growth rate of coots and wood ducks as functions of contaminant exposure.

12. Brown, G. M. Jr.; Hammack, J., and Tillman, M. Mallard population dynamics and management models. *Journal of Wildlife Management*. 1976; 40(3):542-555.
Note: Application of classical fisheries methods to mallard populations. Beverton-Holt model, with carrying capacity a function of habitat quantity. Calculates MSY for humnting. Comparison to previously used "empirical" techniques.

13. Brown, J. H. and A. Kodric-Brown. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*. 1977; 58:445-449.
Note: metapopulation model.

14. Cacho, O. J. Protein and fat dynamics in fish: a bioenergetic model applied to aquaculture. *Ecological Modelling*. 1990; :33-56.
Note: Individual-based bioenergetic model of catfish - separate fat & protein compartments.

15. Cantwell, M. D. and R. T. T. Forman. Landscape graphs: ecological modeling with graph theory to detect configurations common to diverse landscapes. *Landscape Ecology*. 1993; 8(4):239-255.
Note: Network analysis of landscape patterns. Application of graph theory to "pattern recognition" problem in landscape characterization.

16. Caswell, H. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sunderland, MA: Sinauer; 1989; p. 328 pp.
Note: Classic textbook/review of matrix population models. Includes thorough literature review up through late 1980s.

17. Chesser, R. K.; K. B. Williams, and N. E. Mathews. Impacts of toxicants on population dynamics and gene diversity in avian species. *Wildlife Toxicology and Population Modeling*, Kendall, R. J. and T. E. Lacher, Jr. Boca Raton, Florida: Lewis Publishers; 1994; pp. 171-188.
Note: Includes three types of models and analyses: (1) an individual-based bird population model with sex, genotype, toxicant body burden, and reproductive rate as individual characteristics. Includes stochastic variation in mortality and reproduction. Model "experiments" used to investigate influence of toxicant body burden, toxicant critical level, and population carrying capacity on average population size and loss of genetic variablility. (2) Logistic model used to estimate time-of-recovery as a function of mortality level and intrinsic population growth rate. (3) Population genetics theory used to estimate influence of contaminant-induced mortality on effective population size, and consequently on the rate of loss of genetic variation.

18. Cobb, G. P. and M. J. Hooper. Nonlethal wildlife monitoring to determine exposure to xenobiotics and resulting impacts. *Wildlife Toxicology and Population Modeling*, Kendall, R. J. and T. E. Lacher Jr. Boca Raton, FL: Lewis Publishers; 1994; pp. 35-46.
Note: Describes empirically-based models of uptake of diazinon from the gastrointestinal tract; empirical relationships between GI concentration of diazinon and bird mortality; biochemical indicators of pesticide exposure (alkylphosphate excretion, plasma AChE).

19. Conroy, M. J. Y. Cohen F. C. James Y. G. Matsinos and B. A. Maurer. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecological Applications*. 1995; 5(1):17-19.
Note: Reveiw of parameter estimation methods for Spatially explicit population models.

20. Cowan, J. H. Jr. and K. A. Rose. Individual-based model of young-of-the-year striped bass population dynamics. II. Factors affecting recruitment in the Potomac River, Maryland. *Transactions of the American Fisheries Society*. 1993; 122:439-458.
Note: Analysis of individual-based striped bass model, emphasizing environmental influences on year-class strength.

21. Cowan, J. H. K. A. Rose E. S. Rutherford and E. D. Houde. Individual-based model of young-of-the-year striped bass population dynamics. II. Factors affecting recruitment in the Potomac River, Maryland. *Transactions of the American Fisheries Society*. 1993; 122:459-466.

22. Cullen, Murray C. and Connell, Des W. Pesticide Bioaccumulation in Cattle. *Ecotoxicology and Environmental Safety.* 1994; **28**:221-231.
    Note: Pharmacokinetic model of pesticide bioaccumulation in grazing food chain. Suitable for inclusion in individual-based models.

23. Dale, V. H. and R. H. Gardner. Assessing regional impacts of growth declines using a forest succession model. *Journal of Environmental Management.* 1987; **24**:83-93.
    Note: Individual-based forest stand model used to simulate forest die-back in New England.

24. Danielson, B. J. Communities in a landscape: the influence of habitat heterogeneity on the interaction between species. *American Naturalist.* 1991; **138**:1105-1120.

25. DeAngelis, D. L. What food web analysis can contribute to wildlife toxicology. *Wildlife Toxicology and Population Modeling,* Kendall, R. J. and T. E. Lacher, Jr. Boca Raton, Florida: Lewis Publishers; 1994; pp. 365-382.
    Note: General overview of food web theory and analysis. Discusses uses, information requirements of different approaches.

26. DeAngelis, D. L. and L. J. Gross eds. *Individual-Based Models and Approaches in Ecology.* New York: Chapman and Hall; 1992.
    Note: Edited volume containing 23 papers on various aspects of individual-based modeling. Includes overviews of concepts, mathematical techniques, specific applications.

27. DeAngelis, D. L. K. A. Rose L. Crowder E. Marschall and D. Lika. Fish cohort dynamics: Application of complementary modeling approaches. *American Naturalist.* 1993; **68**:273-292.

28. DeAngelis, D. L. L. L. Godbout and B. J. Shuter. An individual-based approach to predicting density-dependent compensation in smallmouth bass populations. *Ecological Modelling.* 1991; **57**:91-115.
    Note: Model of a smallmouth bass population formulated in terms of the reproduction, development, growth, foraging, and survival of individual fish. Calibrated to data on the smallmouth bass population in Lake Opeongo, Ontario. Simulates production of a single year-class from spawning through overwintering survival. Includes influence of environmental conditions and size/health of nest-guarding males.

29. deKroon, H. A. Plaisier J. Van Groenendael and H. Caswell. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology*. 1986; *67*:1427-1431.
Note: Provides definition and rationale for "elasticity" index, a measure of the influence of different life-cycle parameters on the rate of growth of a population.

30. den Boer, P. J. The survival of populations in a heterogeneous and variable environment. *Oecologia*. 1981; **50**:39-53.
Note: Simulation of beetle population fluctuations: simple autocorrelation model based on 20+ years of empirical data on abundance of subpopulations of beetles on a heath. Demonstration that species composed of mutliple independent subpopulations can persist for long time periods in spite of high variability within subpopulations.

31. DiGiulio, R. T.; Washburn, P. C.; Wenning, R. J.; Winston, G. W., and Jewell, C. S. Biochemical responses in aquatic animals: a review of determinants of oxidative stress. *Environmental Toxicology and Chemistry*. 1989; **8**:1103-1123.
Note: Review of biomarker studies: markers of exposure to free-radical-producing chemicals. Discusses methodological problems; limitations on use in regulation. Possibly relevant to development if individual-based models of contaminant effects.

32. Doak, D.; Kareiva, P., and Klepetka, B. Modeling population viability for the desert tortoise in the western Mojave desert. *Ecological Applications*. 1994; **4**:446-460.

33. Dobson, A. and P. Hudson. Assessing the impact of toxic chemicals: temporal and spatial variation in avian survival rates. *Wildlife Toxicology and Population Modeling*, Kendall, R. J. and T. E. Lacher, Jr. Boca Raton, FL: Lewis Publishers; 1994; pp. 85-98.
Note: Describes sources of variation in bird survival: interspecific variation, geographic variation, age-dependent variation, and seasonal variation. No models. Developed from long-term banding studies of common British bird species.

34. Dunning, J. B. B. J. Danielson and H. R. Pulliam. Ecological processes that affect populations in complex landscapes. *Oikos*. 1992; 65169-175.

35. Dunning, J. B. D. J. Stewart B. J. Danielson B. R. Noon T. L. Root R. H. Lamberson and E. E. Stevens. Spatially explicit population models: current forms and future uses. *Ecological Applications*. 1995; 5:3-11.
Note: Overview of spatially-explicit populations models. Lots of references.

36. Ebenhard, T. Colonization in metapopulations: a review of theory and observations. *Biological Journal of the Linnaean Society*. 1991; 42:105-121.
Note: metapopulation models.

37. Ellison, A. M. and B. L. Bedford. Response of a wetland vascular plant community to disturbance: a simulation study. *Ecological Applications*. 1995; 5:109-123.
Note: Wetland ecosystem simulation model, based on cellular automata. Integrates plant life history and population biology with hydrology.

38. Emlen, J. M. Terrestrial population models for ecological risk assessment: a state-of-the-art review. *Environmental Toxicology and Chemistry*. 1989; 8:831-842.
Note: Good review of models of terrestrial animal populations. Emphasizes age-structured models.

39. Emlen, John M. Pikitch Ellen K. Animal Population Dynamics: Identification of Critical Components. *Ecological Modeling*. 1989; 44:253-273.
Note: Stage-based models of terrestrial vertebrate populations. Attempts to identify "critical life stages" for large, long-lived vs. small, short-lived organisms.

40. Fahrig, L. and G. Merriam. Habitat patch connectivity and population survival. *Ecology*. 1985; 66:1762-1768.
Note: metapopulation models

41. Graham, R. L.; Hunsaker, C. T.; O'Neill, R. V., and Jackson, B. L. Ecological risk assessment at the regional scale. *Ecological Applications*. 1991; 1:196-206.
Note: Application of risk analysis concepts to landscape-level problems. Includes analysis (hypothetical) of impacts of air pollution and bark beetle infestations on forest landcover.

42. Gurney, W. S. C. E. McCauley R. M. Nisbet and W. W. Murdoch. The physiological ecology of *Daphnia*: a dynamic model of growth and reproduction. *Ecology*. 1990; 71:716-732.
Note: Individual-based model of *Daphnia* population growth derived from a physiological model of the individual organisms. The individual model is described in a companion paper by McCauley et al. (1990) in the same issue.

43. Gustafson, E. J. and T. R. Crow. Modeling the effect of forest harvesting on landscape structure and the spatial distribution of cowbird brood parasitism. *Landscape Ecology*. 1994; 9:237-248.
Note: Influence of timber harvesting patterns and resulting landscape structure on the vulnerability of neotropical migrant nests to cowbird parasitism.

44. Hallam, T. G.; Clark, C. E., and Lassiter, R. R. Effects of Toxicants on Populations:A Qualitative Approach I. Equilibrium Environmental Exposure. *Ecological Modeling*. 1983; 18:291-304.
Note: Individual-based model of Daphnia population exposed to contaminants.

45. Hallam, T. G. and J. T. DeLuna. Effects of Toxicants on Populations:a Qualitative Approach III. Environmental and Food Chain Pathways. *Journal of Theoretical Biology*. 1984; 109:411-429.
Note: Individual-based Daphnia population model based on three-compartment model of contaminant uptake and toxicity.

46. Hallam, T. G., and J. T. DeLuna.. Extinction and Persistance in Models of Population-Toxicant Interactions. *Ecological Modeling*. 1983; 22:13-20.

47. Hallam, T. G.; Lassiter, R. R.; Li, J., and McKinney, W. Toxicant-induced mortality in models of Daphnia populations. *Environmental Toxicology and Chemistry*. 1990; 9:597-621.
Note: Incorporation of contaminant pharmacokinetics/pharmacodynamics in Hallam's individual-based Daphnia model.

48. Hallam, T. G.; Lassiter, R. R.; Li, J., and Suarez, L. A. Modelling individuals employing an integrated energy response: application to Daphnia. *Ecology*. 1990; 71:938-954.
Note: Bioenergetic model of Daphnia life cycle. Basis for Hallam's individual-based Daphnia population model.

49. Hanski, I. and M. Gilpin. Metapopulation dynamics: a brief history and conceptual domain. *Biological Journal of the Linnaean Society*. 1991; 423-16.
Note: Nice review of metapopulation theory, from Andrewartha and Birch through the date of publication.

50. Hansson, L. Dispersal and connectivity in metapopulations. *Biological Journal of the Linnaean Society*. 1991; 42:89-103.

51. Holt, R. D. S. W. Pacala T. W. Smith and J. Lu. Linking contemporary vegetation models with spatially explicit animal population models. *Ecological Applications*. 1995; 5:20-27.
Note: Discussion of issues involved in linking vegetation dynamics to population dynamics.

52. Huston, M. A. and T. M. Smith. Plant succession: life history and competition. *American Naturalist*. 1987; 130:168-198.
Note: Uses forest-stand model to explain alternative tree life-history strategies in terms of competition for space and light.

53. Jager, H. I. D. L. DeAngelis M. J. Sale W. Van Winkle D. D. Schmoyer M. J. Sabo D. J. Orth and J. A. Lukas. An individual-based model for smallmouth bass reproduction and young-of-the-year dynamics in streams. *Rivers*. 1993; 4:491-113.
Note: Modification of original DeAngelis et al. smallmouth bass model. Major innovation consists of incorporation of spatial location and movement as individual descriptors. Based on data from North Anna River, Virginia.

54. Kareiva, P. Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs*. 1982; 52:261-282.

55. Kooijman, S. A. L. M. and Metz, J. A. J. On the Dynamics of Chemically Stressed Populations:The Deduction of Population Consequences from Effects on Individuals. *Ecotoxicology and Environmental Safety*. 1984; 8:254-274.
Note: A general and explicit model for the age dependent growth and reproduction of individuals as a function of food supply.

56. Lacy, R. C. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection and population subdivision. *Conservation Biology*. 1987; 1:143-158.
Note: Generalized metapopulation model.

57. Lacy, R.C.. VORTEX: a computer simulation model for use in population viability analysis. *Wildlife Research*. 1993; 20:45-65.
Note: An individual-based model of the dynamics of small populations - has a metapopulation version that can simulate up to 20 interacting subpopulations.

58. Lamberson, R. H. B. R. Noon C. Voss and K. McKelvey. Reserve design for terrestrial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. *Conservation Biology*. 1994; 8:185-195.
Note: Metapopulation model of Northern spotted owl.

59. Lamberson, R. H. R. McKelvey B. R. Noon and C. Voss. A dynamic analysis of Northern Spotted Owl viability in a fragmented forest landscape. *Conservation Biology*. 1992; **6**:505-512.
    Note: Analysis of influence of landscape structure on Northern Spotted Owl metapopulation.

60. Lande, R. Demographic models of the northern spotted owl (Strix occidentalis caurina). *Oecologia*. 1988; **75**:601-607.
    Note: Application of (1) Mertz's life table approach, and (2) Levins' patch dynamics approach to survival of spotted owl. Argues that the population is currently approximately stable based on life table statistics. Argues that USDA management plan will not preserve sufficient habitat to prevent extinction in the future.

61. Lande, R. Extinction thresholds in demographic models of terrestrial populations. American Naturalist. 1987; **130**:624-635.

62. Lassiter, R. R. and and T.G. Hallam. Survival of the fattest: implications for acute effects of lipophilic chemicals on aquatic populations. *Environmental Toxicology and Chemistry*. 1990; **9**:585-596.
    Note: Pharmacokinetic model of uptake and effects of lipophilic chemicals on fish; suitable for incorporation in individual-based population models.

63. Law, R. A model for the dynamics of a plant population containing individuals classified by age and size. *Ecology*. 1983; **64**:224-230.
    Note: First good integration of age and size in a population model.

64. Law, R. and M. T. Edley. Transient dynamics of populations with age- and size-dependent vital rates, *Ecology* 1990; **71**:1863-1970.
    Note: Analysis of Law's age/stage-structured model.

65. Leonardsson, K. Long-term ecological effects of bleached pulp-mill effluents on benthic macrofauna in the Gulf of Bothnia. *Ambio*. 1993; **22**:359-362.
    Note: Sublethal effects of contaminants on benthic predator-prey system/ combines modeling, lab experiments, field monitoring.

66. Li, H. J. F. Franklin F. J. Swanson and T. A. Spies. Developing alternative forest cutting patterns: a simulation approach. *Landscape Ecology*. 1993; **8**:63-75.
    Note: Examination of effects of different forest cutting patterns on habitat fragmentation in managed forest landscapes.

67. Lindenmayer, D. B. and R. C. Lacy. Metapopulation viability of arboreal marsupials in fragmented old-growth forests: comparison among species. *Ecological Applications*. 1995; 5:183-199.
Note: Comparison of metapopulation viability for different Australian possum species; relation to life-history parameters.

68. Lindenmayer, D. B., and R. C. Lacy. Metapopulation viability of Leadbeater's possum, Gymnobelideus leadbeateri, in fragmented old-growth forests. *Ecological Applications*. 1995; 5:164-182.
Note: Application of VORTEX to viability of G. leadbeateri.

69. Lindenmayer, D. B. Clark T. W. Lacy R. C. Thomas V. C. Population viability analysis as a tool in wildlife conservation policy: with reference to Australia. *Environmental Management*. 1993; 17:745-758.
Note: Nice overview of PVA.

70. Liu, J. An introduction to ECOLECON: a spatially-explicit model for ECOLogical ECONomics of species conservatin in complex forest landscapes. *Ecological Modelling*. 1993; 70:63-87.
Note: Extension of Pulliam's BACHMAP model to include (1) GIS-based landscape characteristics and (2) timber harvest economics.

71. Liu, J. J. B. Dunning and H. R. Pulliam. Assessing alternative management strategies: an example coupling GIS with spatially-explicit models. *Conservation Biology*. (in press).
Note: Spatially-explicit population model linked to GIS.

72. Loza, H. J. W. E. Grant J. W. Stuth and T. D. A. Forbes. Physiologically based landscape use model for large herbivores. *Ecological Modeling*. 1992; 61:227-252.
Note: Links physiologically-based model of cow foraging behavior to range landscape model. Method potentially applicable to wildlife foraging in agriculture-dominated landscapes.

73. Madenjian, C. P. and S. R. Carpenter. Individual-based model for growth of young-of-the-year walleye: a piece of the recruitment puzzle. *Ecological Applications*. 1991; 1:268-278.
Note: Model of year-class production in walleye, modeling approach is similar to the DeAngelis et al. smallmouth bass model.

74. Maurer, B. A. Dipodomys populations as energy-processing systems: regulation, competition, and hierarchical organization. *Ecological Modelling*. 1990; 50:157-176.
    Note: Two-species, energetics-based compartment model. Good application of Odum-style ecology.

75. McCauley, E. W. W. Murdoch R. M. Nisbet and W. S. C. Gurney. Thy physiological ecology of *Daphnia*: development of a model of growth and reproduction. *Ecology*. 1990; 71:703-715.
    Note: Development and testing of a model of the growth and reproduction of individual *Daphnia*. A companion paper (Gurney et al. 1990) used the model as a foundation for an individual-based *Daphnia* population model.

76. McKelvey, K. B. B. R. Noon R. H. Lamberson. Conservation planning for species occupying fragmented landscapes: the case of the northern spotted owl. IN: *Biotic Interactions and Global Change*, Karieva, P. M. ,J. G. Kingsolver, and R. B. Huey (eds.). Boston, MA: Sinauer; 1992; pp. 424-450.

77. Messier, F. Ungulate population models with predation: a case study with North American moose. *Ecology*. 1994; 75:478-488.
    Note: moose-wolf population models and results.

78. Meyer, J. S. and M. S. Boyce. Life historical consequences of pesticides and other insults to vital rates. IN: *Wildlife Toxicology and Population Modeling*, Kendall, R. J. and T. E. Lacher, Jr. (Eds.) Boca Raton, Florida: Lewis Publishers; 1994; pp. 349-363.
    Note: Life-table analysis of bird populations using the Euler equation: estimation of sensitivity of lambda to changes in fecundity and survivorship, given different age/size structures. Some new references.

79. Miller, N. L. Stability analysis of toxic substances within aquatic ecosystems and their effect on aquatic populations. *Ecological Modelling*. 1992; 60:151-165.
    Note: 11-compartment model of vinyl chloride in an aquatic ecosystem; includes Lotka-Volterra planktivorous fish model.

80. Mittelbach, G. G. and Osenberg, C. W. Stage-structured interactions in bluegill: consequences of adult resource variation. *Ecology*. 1993; 74:2381-2394.
    Note: Classic study of bluegill population biology, emphasizing differences in habitat selection and growth rates between juveniles and adults. Uses two-stage population model.

81. Morgan, M. J. and Kiceniuk, J. W. Effect of fenitrothion on the foraging behavior of juvenile Atlantic salmon. *Environmental Toxicology and Chemistry.* 1990; 9:489-495.
Note: Effects of sublethal exposure on foraging behavior (including dose-response relationships). Suitable for inclusion in individual-based population models.

82. Murdoch, W. W. Population regulation in theory and practice. *Ecology.* 1994; 75:271-287.
Note: Review of theory and field results on population regulation; reconciliation of Nicholson/Bailey with Andrewartha/Birch; argument that stage-based/natural-history-related approaches are most fruitful avenue to pursue at this time. Great references to recent literature.

83. Murphy, D. D. and B. R. Noon. Integrating scientific methods with habitat conservation planning: reserve design for Northern Spotted Owls. *Ecological Applications.* 1992; 2:3-17.

84. O'Connor, R. J. Population patterns and process parameters - issues in integrating monitoring and models. IN: *Wildlife Toxicology and Population Modeling,* Kendall, R. J. and T. E. Lacher, Jr. (eds.) Boca Raton, Florida: Lewis Publishers; 1994; pp. 283-300.
Note: Good qualitative discussion of density-dependence and habitat-dependent population dynamics in birds. Good references to bird population dynamics literature.

85. Oliver, George R. and Laskowski, Dennis A. Development of Environmental Scenarios for Modeling the Fate of Agricultural Chemicals in Soil. *Environmental Toxicology and Chemistry.* 1986; 5:225-231.
Note: Used computerized soil survey information to identify soils most likely to be encountered in major use areas. A climatic model generated rainfall patterns for the study areas and provided the probability statement for the environmental assessment. Approach applicable to development of spatially-explicit population models for pesticide risk assessment.

86. Oritsland, N. A. and Markussen, N. H. Outline of a physiologically based model for population energetics. *Ecological Modelling.* 1990; 52:267-288.
Note: Physiological model of harp seals. Thermoregulatory requirements, growth, feeding requirements. Linked to population via Leslie matrix.

87. Ostendorf, B. and J. F. Reynolds. Relationships between a terrain-based hydrologic model and patch-scale vegetation patterns in an arctic tundra landscape. *Landscape Ecology.* 1993; 8:229-237.
Note: Model predicts hydrology, which is then correlated with vegetation data.

88. Pulliam, H. R. Incorporating concepts from population and behavioral ecology into models of exposure to toxins and risk assessment. IN: *Wildlife Toxicology and Population Modeling*, Kendall, R. J. and T. E. Lacher Jr. (eds.) Boca Raton, FL: Lewis Publishers; 1994; pp. 13-26.
Note: Review of applicability of foraging theory and habitat structure models to the development of population exposure and effects models. Includes metapopulation theory. Case study using Pulliam's study of Bachmann's sparrow on the Savannah River Site.

89. Pulliam, H. R. J. B. Dunning Jr. and J. Liu. Population dynamics in complex landscapes: a case study. *Ecological Applications.* 1992; 2:165-167.
Note: Spatially explicit Population Model pf Bachman's Sparrow population on DOE Savannah River Site.

90. Reckhow, K. H. and S. C. Chapra. Confirmation of water quality models. *Ecological Modeling* 20:113-133.
Note: Philosophy of hypothesis testing: suggestions of statistical techniques for comparing model output to observational data. Good application of Bayesian approach - possibly applicable to testing of pesticide effects models.

91. Rice, J. A. L. B. Crowder and K. A. Rose. Interactions between size-structured predator and prey populations: Experimental test and model comparison. *Transactions of the American Fisheries Society.* 1993; 122:481-491.

92. Rice, J. A. T. J. Miller K. A. Rose L. B. Crowder E. A. Marschall A. S. Trebitz and D. L. DeAngelis. Growth rate variation and larval survival: Implications of an individual-based size-dependent model. *Canadian Journal of Fisheries and Aquatic Sciences.* 1993; 50:133-142.

93. Rose, K. A. J. H. Cowan E. D. Houde and C. C. Coutant. Individual-based modeling of environmental quality effects on early life stages of fish: a case study using striped bass. *American Fisheries Society Symposia,* 1993; 14:125-145.

94. Rose, K. A. S. W. Christensen and D. L. DeAngelis. Individual-based modeling of populations with high mortality: A new method for following a fixed number of model individuals. *Ecological Modelling.* 1993; 68:273-292.

95. Rose, K. P. and J. H. Cowan Jr. Individual-based model of young-of-the-year striped bass population dynamics. I. Model description and baseline simulations. *Transactions of the American Fisheries Society.* 1993; **122**:415-438.
Note: Description of individual-based striped bass population model; basic structure analogous to DeAngelis et al. smallmouth bass model, but the principal emphasis is on early larval survival.

96. Samuels, William B. and Ladino, Anthony. Calculations of Seabird Population Recovery from Potential Oilspills in the Mid-Atlantic Region of the United States. *Ecological Modeling.* 1983; **21**:63-84.
Note: Model of herring gull and common tern population recovery from potential oilspill damage in the US mid-Atlantic Outer Continental Shelf (OCS) oil leasing area. Reviewed in detail by Barnthouse (1993).

97. Schaefer, E. W. Jr. Comparative avian toxicology: What is its role in predicting and monitoring the effects of agricultural pesticides? IN: *Wildlife Toxicology and Population Modeling,* R. J. Kendall and T. E. Lacher, Jr. (eds.) Boca Raton, Florida: Lewis Publishers; 1994; pp. 321-337.
Note: Review of comparative toxicology studies. Concludes that (1) species sensitivites to the same pesticide vary over 2-3 orders of magnitude, (2) there is no reliably "most sensitive" species, (3) therefore, extrapolation is impossible [this was also at one time the consensus opinion among fish toxicologists]. Instead, increase post-registration monitoring is needed.

98 Simberloff, D. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics.* 1988; **19**:473-511.
Note: Critical review of relevance of theoretical models to conservation of small populations; calls for more autecological studies.

99. Slade, N. A. Models of structured populations: age and mass transition matrices. IN: *Wildlife Toxicology and Population Modeling,* Kendall, R. J. and T. E. Lacher, Jr. (eds.) Boca Raton, Florida: Lewis Publishers; 1994; pp. 189-199.
Note: Overview of age and size-structured matrix models. One example. Some new references.

100. Sterbacek, Z.; Skopek, V., and Zavazal, V. A composite landscape ecology prognostic expert system - COLEPES. Part I. System philosophy and design. *Ecological Modelling.* 1990; **50**:145-156.
Note: Description of expert system that uses quantitative environmental models as subcomponents - few details provided.

101. Tipton, Alan R.; Kendall, Ronald J.; Coyle, John F., and Scanlon, Patrick F. A Model of the Impact of Methyl Parathion Spraying on a Quail Population. *Bulletin of Environmental Contamination and Toxicology.* 1980; **25**:586-593.
Note: Novel application of matrix population model to acute pesticide exposures. Reviewed in depth by Barnthouse (1993).

102. Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics.* 1989; **20**:171-197.
Note: General review of landscape ecology.

103. Turner, M. G. G. J. Arthaud R. T. Engstrom S. J. Hejl J. Liu S. Loeb and K. McKelvey. Usefulness of spatially explicit population models in land management. *Ecological Applications.* 1995; **5**:12-16.
Note: Overview of use of SEPMs in land management.

104. Turner, M. G. Y. Wu W. H. Romme and L. L. Wallace. A landscape simulation model of winter foraging by large ungulates. *Ecological Modelling.* 1993; **69**:163-184.
Note: Description of spatially-explicit population model for elk and deer in Yellowstone National Park.

105. Turner, M. G. Y. Wu W. H. Romme L. L. Wallace and A. Brenkert. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecological Applications.* 1994; **4**:472-496.
Note: Uses spatially explicit population model to evaluate influence of fire and climatic variability on survival of ungulate populations in Yellowstone National Park.

106. Turner, Monica G; R, Costanza, and F. H. Sklar. Methods to evaluate the performance of spatial simulation models. *Ecological Modelling.* 1989; **48**:1-18.
Note: Comparison of different methods of quantifying spatial patterns.

107. Tyler, J. A. and K. A. Rose. Individual variability and spatial heterogeneity in fish population models. *Review in Fish Biology and Fisheries.* 1994; 491-123.

108. Urban, D. L. and T. M. Smith. Microhabitat pattern and the structure of forest bird communities. *American Naturalist.* 1989; **133**:811-829.