

# Concepts from complex adaptive systems as a framework for individual-based modelling

Steven F. Railsback \*

*Lang, Railsback and Associates, 250 California Avenue, Arcata, CA, 95521 USA*

Received 26 June 2000; received in revised form 28 November 2000; accepted 28 November 2000

---

## Abstract

Individual-based models (IBMs) have long been proposed as a key tool for understanding and predicting ecosystem complexities, yet the contribution of this approach to basic or applied ecology has been less than anticipated. Fundamental reasons for the disappointing contribution of IBMs have been, in the current absence of a theoretical foundation for IBMs, conceptual flaws in model formulation and the failure to address critical computer implementation issues. Researchers in the new field of Complex Adaptive Systems (CAS) study how complex behaviors emerge in systems of relatively simple interacting individuals. Research on CAS, while still new and informal, has identified key concepts for making individual-based systems realistic. I propose that explicit consideration of the following concepts from CAS should make the design of IBMs less ad hoc and more likely to produce models of value for basic and applied ecology: (1) *Emergence*: what behaviors and population dynamics should emerge from the model's mechanistic representation of key processes vs. being imposed on the model as empirical relations? How should individual traits be modeled so that realistic population responses emerge?; (2) *Adaptation*: given the model's temporal and spatial scales, what adaptive processes of individuals should be modeled? What mechanisms do individuals use to adapt in response to what environmental forces?; (3) *Fitness and strategy*: what measures of fitness are appropriate to use as the basis for modelling decision making? Should fitness measures change with life history state?; (4) *State-based responses*: how should decision processes depend on an individual's state?; (5) *Prediction*: anticipating decision outcomes appears essential for modelling many behaviors; what are realistic assumptions about how organisms predict the consequences of decisions?; (6) *Computer implementation*: what user interfaces are necessary to make the model, and especially individual behaviors, observable and testable? How will the model's full design and computer implementation be documented and tested so results are reproducible and valid? © 2001 Elsevier Science B.V. All rights reserved.

*Keywords*: Complex adaptive systems; Individual-based model; Modelling theory; Emergence; Adaptation; Fitness; State-based decisions; Prediction; Computer implementation

---

## 1. Introduction

The individual-based modelling approach has to date been less productive for ecological re-

\* Tel.: +1-707-8220453; fax: +1-707-8221868.

*E-mail address*: ira@northcoast.com (S.F. Railsback).

search and management than many ecologists expected. At the same time that ecologists were realizing the important effects of complex natural phenomena and the limitations of conventional differential equation-based models for dealing with complexities (Patten and Jørgensen, 1995), individual-based models (IBMs) were hailed as an approach that was naturally suited for the new ecology (Huston et al., 1988). However, the contribution of IBMs to ecological research and management to date has been minor (Grimm, 1999). Even a casual review of journal articles and conference presentations shows that IBMs have certainly not displaced conventional modelling approaches and are, in fact, used relatively rarely for research and management.

Also in the 1990s, the new scientific field of Complex Adaptive Systems (CAS) established itself with a focus on how the properties of aggregations of individuals can be determined by the characteristics and behavior of the individuals. To date, most work in CAS has been conducted in highly abstracted and artificial systems like cellular automata and genetic computer algorithms, and in the fields of economics, sociology, microbiology, and medicine. Although CAS is in its infancy and remains in search of fundamental principles (Auyang, 1998), basic concepts from CAS can be extracted from its literature.

The specific objectives of this paper are to (a) demonstrate that an important reason why the individual-based approach to ecological modelling has not proven to be as productive as anticipated is the lack of a theoretical framework, and (b) present some key concepts of CAS that may be valuable as a way of thinking about, designing, and evaluating IBMs. My more fundamental goal is to encourage discussion among ecological modellers about frameworks and theory for individual-based approaches. Most of the examples and literature discussed in this paper are from models of vertebrate (mainly, fish) behavior because I am most familiar with these models; however, the concepts and conclusions apply to models addressing a wide range of organisms, scales, and ecological issues.

## 2. Background

### 2.1. Individual-based modelling

The landmark paper of Huston et al. (1988) identified the promise of IBMs for naturally and easily simulating effects of individual variation, spatial processes, cumulative stresses, and many other natural complexities. The basic concept of IBMs is simple and appealing: build a model of an individual organism, build a model of the environment, and let a computer create multiple individual organisms and simulate the interactions of the individuals with each other and the environment. In many ways, building a model of an individual organism is easier than building a model of a population: individuals can be tested in controlled ways that populations cannot, and are more limited in their range of responses and therefore more predictable in their behavior than are populations (Rose, 2000).

Despite these advantages, using IBMs has so far not been a very productive approach to ecology or ecological management. Early attention to potential problems with IBMs was drawn by Murdoch et al. (1992), Bart (1995). The extensive reviews of Grimm (1999), Grimm et al. (1999) conclude that IBMs have not yet fulfilled the promise identified by Huston et al., in large part because many models have been built without sufficient attention to the appropriateness of the assumptions used. Railsback et al. (1999) provide an example analysis of several published models, illustrating concerns with the critical rules for determining how animals select habitat. This literature indicates two root reasons why few IBMs have proven useful or gained acceptance with ecologists and managers.

The first reason why IBMs have been unproductive is inadequate attention to ‘toolmaking’ — computer implementation — issues, especially the failure to encode models in software that allows the behavior of the model’s individuals to be observed and tested. I address this issue below (Computer simulation).

The second root reason that IBMs have been unproductive is that inappropriate assumptions abound in IBMs. Modellers have almost univer-

sally taken an ad hoc approach to building IBMs, drawing various model components from existing literature or field observations with little thought to each component's appropriateness to an overall approach. One of the advantages of IBMs mentioned above, that models of individuals can be easier to build, has often become a disadvantage in practice: the apparent ease of writing a model of an individual organism promotes inadequate attention to assumptions or understanding of their consequences. The following classes of mistakes are common in IBMs. (1) Using model components developed originally for one set of assumptions to simulate conditions under which those assumptions clearly are not met. An example (discussed further below, Section 3.1) is modelling habitat selection by minimizing the ' $\mu/g$ ' ratio of mortality risk to growth rate; this approach was taken from a derivation based on specific assumptions that are often violated in IBMs (Railsback et al., 1999); (2) applying relations and parameters developed for one spatial or temporal scale to other scales that they are not appropriate for, a concern with all ecological models; (3) embedding empirical relations in models that are purported to be mechanistic. Mixing empirical and mechanistic models is always a conceptual concern (Mangel et al., In press). It can be a serious source of error when empirical relations are included in models that are then used to simulate conditions far different from those under which the empirical relations were developed; (4) confusing individual - and population-level parameters. An example of this kind of mistake is assuming that a population-level mortality rate can be used as the mortality probability of individuals. The mortality rate of a population is a complex function of the individuals, their varying vulnerabilities, and environmental conditions. A population with a starvation rate of 50% may include a minority of dominant individuals with very little probability of starvation plus a majority of subordinate individuals with a probability of starving that starts high but decreases as others die and competition for food decreases. In a population exhibiting 50% starvation, few if any individuals may have a starvation probability of 50% at any time. This variation among individu-

als can have important effects on model predictions (Grimm et al., 1999; Uchmanski, 1999, 2000).

It is not surprising that many IBMs contain serious conceptual errors because there is little literature on how to build successful IBMs. The IBM literature offers numerous model descriptions but few tests of models (but see Railsback and Harvey, In prep.), and little discussion of general modelling approaches (Murdoch et al., 1992; Grimm, 1999; Grimm et al., 1999; Thulke et al., 1999) or specific methods for modeling important processes (Railsback et al., 1999). To my knowledge, individual-based approaches are rarely addressed thoroughly in ecology or ecological modelling textbooks or classes. Conventional ecological models are firmly grounded in the established framework of differential calculus. In contrast, we currently lack a set of guidelines or concepts that would help IBM designers identify and avoid inappropriate assumptions; we lack even a list of issues or questions to think about when building or reviewing these models.

## 2.2. Complex adaptive systems

Understanding and analyzing systems as the complex emergent properties of adaptive individuals is a new and potentially revolutionary way of approaching a number of sciences. The essence of CAS is the study of systems built of individual agents that are capable of adapting as they interact with each other and with an environment, and especially the attempt to understand how the characteristics of individuals affect the system-level responses (Auyang, 1998). The focus of CAS research has been from the bottom up, describing kinds of agents and environments and then experimentally finding out what kind of complex dynamics are exhibited by the system of agents.

Much of the work in CAS has been in search of fundamental concepts or laws describing the behavior of complex systems (Kauffman, 1995), or in examining the potential capabilities and 'intelligence' of artificial complex systems (Holland, 1995, 1998). (One interesting aspect of CAS is that, because of the field's newness, potential impact, and fundamental nature, much of the pri-

mary literature is in popular, accessible books.) Well-known CAS models include: (1) the ‘boids’ model of C. Reynolds, in which flocking behavior emerges in collections of individuals following three simple rules (Waldrop, 1992); (2) cellular automata, grids of individual cells that change state (e.g. ‘off’ vs. ‘on’) in response to the state of their neighboring cells; (3) autocatalytic sets of chemicals, suggested by Kauffman (1995) as a phenomenon making the genesis of life likely; and (4) genetic computer algorithms that use mutation and competitive selection to evolve solutions to difficult problems.

Some CAS research has been in the context of sciences like archaeology (Kohler et al., 1999), computer science (Forrest, 1990), economics (Fama, 1991), microbiology (Devreotes, 1989; Kreft et al., 1998), and sociology (Goldspink, 2000). Surprisingly little application of CAS has been in ecology (but see, e.g. Booth, 1997). The purpose of this paper is not to propose more CAS-based studies in ecology, although such studies would likely be exciting and fruitful. Nor is my purpose to critically evaluate CAS research and models, which have sometimes suffered from the same kinds of problems ecological IBMs have suffered from. Instead, I identify some concepts that appear common in CAS research and explore how they can serve as a framework for designing IBMs for ecological research and applications.

The study of CAS seems a natural source of analogies for IBMs. Whereas ecology has historically had a system-level perspective, CAS explicitly addresses the traits of individuals and how these traits produce system responses. The history of CAS is of researchers examining systems of sometimes extremely simple agents, exploring the system-level consequences of changing the capabilities of agents, and sometimes designing agents to produce certain system-level properties (Waldrop, 1992; Auyang, 1998). The simplicity of the agents used in most CAS research, compared to real organisms, makes it more likely that basic characteristics and themes can be sorted out. Looking at CAS should help us overcome the system-level biases of ecology and the apparently overwhelming complexity of ecosystems, and focus on fundamental aspects of modelling popula-

tion-level phenomena as the emergent properties of individuals.

### 3. CAS concepts and their application to IBMs

From the CAS literature I identified six key concepts that seem clearly applicable to IBMs. Most of these concepts are characteristics of individual agents that appear important to producing complex and lifelike system dynamics. Because these characteristics appear essential to lifelike behavior in even the simplest artificial systems, they deserve consideration in the design of IBMs. The first concept (emergence) is a system-level characteristic, but a result of how individuals are modeled. The final concept concerns tool-making issues that are common between CAS and IBMs.

#### 3.1. Emergence

A defining characteristic of CAS is that system-level properties emerge from the characteristics of individual agents, and that these emergent properties can be far more complex and capable than are the individuals. Examples range from interesting patterns emerging from the simplest cellular automata to the human brain’s function emerging from the limited capabilities of individual neurons. Understanding how system-level properties emerge from the characteristics of individual agents is the fundamental problem of CAS research (Auyang, 1998) and has been described by Levin (1999) as the most important challenge for ecologists.

Models in which complex and realistic system responses emerge naturally from simple individual behaviors should be very appealing to ecologists, because such models are more likely to represent the basic mechanisms driving ecosystems. Being able to predict a wide range of realistic system-level responses from a model in which individuals follow simple decision rules should give us much greater confidence that the model is general and more safely applied to unobserved situations than if numerous complicated rules are needed to force the system-level responses.

This ‘emergent response’ approach to modelling, however, seems contradictory to the inclinations of most ecologists building IBMs. The dominant approach used in IBMs has instead been the use of ‘imposed responses’, in which desired outcomes are forced into the system by telling individuals what to do in specific situations. The reliance of most IBMs on imposed responses is understandable. Faced with the complexity of ecosystems, ecological modellers have historically relied on approaches where models are designed, parameterized, and tested to reproduce observed system-level responses (Hilborn and Mangel, 1997). Therefore, it was natural for early developers of IBMs to write model rules that force individuals and populations to behave in ways that have been observed in the field. Examples include modeling animal movement as a random process that simply reproduces observed movement patterns (Kaiser 1979), requiring fish to always maintain a feeding territory (Van Winkle et al., 1998), and forcing animals to shift habitat when they reach a certain size (Nibbelink and Carpenter, 1998). The IBM approach of Folse et al. (1989) uses a data base of such imposed response rules. Using an observed mortality rate as the mortality probability of individuals is another example of imposing a desired outcome into a model: this approach forces the model to reproduce the observed mortality rate instead of simulating realistic variation in risk.

The problem with imposed responses in an IBM is that they are actually empirical models and, therefore, not reliable when simulating conditions other than those that occurred when the responses were observed. For example, model trout are required to maintain feeding territories because stream trout are often observed to exhibit territorial behavior; this modelling approach encodes the empirical observation of territoriality. Problems arise when the model is used to simulate conditions under which trout are not naturally territorial (e.g. when food availability is highly variable over space so fish congregate in good feeding locations, or in winter when behavior is focused on predator avoidance instead of feeding, or when trout seek refuge from some short-term risk like a flood flow; Nielsen, 1992; Harvey et al.,

1999). Some imposed responses are essential in IBMs; the alternative of mechanistically modeling all of an organism’s behaviors as a mechanistic decision-making process is unlikely to be feasible. Likewise, not all empirical observations should be considered imposed responses if represented directly in an IBM; for example, observations may show that an animal species is so innately territorial that it is best modeled as always maintaining a territory. However, the overuse of imposed responses results in IBMs that are no longer mechanistic models but instead very complex empirical models, often without the author realizing the difference.

A subtle way that imposed responses can find their way into an IBM is through the use of mathematically derived assumptions. The assumption that animals maximize their fitness by selecting habitat that minimizes the  $\mu/g$  ratio of mortality risk to growth rate is an excellent example. Telling animals to select habitat that minimizes  $\mu/g$  appears to be a simple, practical approach for making movement decisions in an IBM. However, the concept that minimizing  $\mu/g$  maximizes fitness was mathematically derived for a very specific, limiting set of conditions (Gilliam and Fraser, 1987). Using  $\mu/g$  in a model implicitly assumes that the conditions used in deriving this approach are true in the model; in reality, though, this assumption is typically violated with serious consequences in IBMs (Railsback et al., 1999; Railsback and Harvey, In prep.). One of the primary advantages of IBMs over differential equation-based models is that simplifying mathematical assumptions are not needed to obtain results (Huston et al., 1988). Modellers should take advantage of the ability of IBMs to directly simulate key processes, avoiding derived simplifications that are based on assumptions likely to be violated.

My colleagues and I experiment with ways to design fish models so that complex and realistic behaviors and group dynamics emerge from simple rules for habitat selection by individuals. When the other concepts discussed below are factored into a model, we find it surprisingly easy to cause such emergence. Two examples from this work contrast the emergent vs. imposed response approaches.

Our primary example of modeling fish behavior as an emergent response is an IBM in which we tell trout simply to select habitat that maximizes a direct indicator of their fitness potential. Basic components of individual fitness are survival and growth to a future reproductive state, so our individuals choose habitat that maximizes their probability of survival and growth to reproductive maturity over an upcoming time horizon of  $T$  days. [Similar approaches were used by Bull et al. (1996), Thorpe et al. (1998).] We do not direct or restrict movement in any other way except for assuming a limit on the area of habitat each fish is familiar with and considers as a potential destination. We provide the fish with simple mechanistic models of how food intake, energetic costs, and mortality risks vary among potential destinations, and make food intake a function of competition with other trout in the same habitat patch. In this model, a wide range of realistic habitat selection patterns emerges in response to changes in physical habitat, predation risks, food availability, temperature, and inter-species competition (Railsback and Harvey, In prep.). Because this range of realistic behaviors emerge naturally from our model, we are more confident that the model is general and applicable to a wide array of conditions than we would be if these patterns were forced into the model by multiple situation-specific rules. In contrast, the model of Nibbelink and Carpenter (1998) uses rules that force fish to shift habitat as they grow; with our approach such habitat shifts emerge without being programmed.

Our model of upstream spawning migration by adult salmon provides a second example of simple rules producing realistic emergent response in an IBM. To model how salmon migrate from the ocean to their spawning ground, a typical ‘imposed response’ approach would be to tell each fish which tributary to select at each tributary junction, perhaps also telling some fraction of the fish to make wrong turns to mimic observed rates of straying. Instead, we based a decision rule on actual salmon navigation mechanisms. The literature indicates that when salmon detect that they are in water containing flow from their natal spawning ground they swim upstream; otherwise

they swim downstream (Hasler and Scholz, 1983). When salmon in our model come to a tributary junction, they make a random decision of which tributary to enter, with probabilities proportional to flow so fish are more likely to follow larger streams. The fish periodically ‘sniff’ whether they are downstream of their natal spawning ground and consequently decide whether to swim upstream or downstream. This approach not only prevents us from having to give each fish a map to its destination (thereby making the model more robust and easier to use), but causes such realistic emergent responses as rapid migration up large rivers, delays and exploration at the mouth of small spawning tributaries, and pulses of migration up spawning tributaries when flows increase.

Designing models so that important responses emerge from simpler mechanisms requires a process for identifying traits (characteristics and decision-making processes) of individual organisms and their habitat that cause such emergence. The modeller may find that the emergent responses are not sufficiently realistic, or that several alternative ways of representing individuals and habitat can cause some realistic emergent responses. The problem of designing models of individual traits so that realistic system-level responses emerge was identified (above) as the fundamental problem in understanding complex systems. Ecologists have little experience with this problem but Auyang (1998) provides a valuable exploration of the general topic. In testing our trout model habitat selection rules (below, Section 3.3) my colleagues and I developed an approach to identifying individual traits that produce realistic population responses (Railsback, In press). Our approach takes advantage of ‘pattern-oriented’ ecological modelling (Grimm et al., 1996) and the ‘synthetic microanalysis’ of Auyang (1998). Briefly, we test models of individual traits by whether they reproduce, in the IBM, a wide range of realistic patterns of emergent response. To my knowledge, our approach is the only one developed for this critical issue in designing IBMs.

When designing an IBM, modellers need to identify observed responses they are imposing and think carefully about whether they are limiting their model’s generality and mechanistic nature.

Even if imposed responses are left in a model (which is often appropriate), they should be carefully documented and the consequences considered. For responses expected to emerge from the traits of model individuals, the modeller should plan analyses to validate that such emergence actually occurs. The potential emergence of realistic behavior and system dynamics from simple individuals in IBMs remains a largely unexplored field, especially for organisms other than salmonids. However, our work to date shows that there are foraging and movement approaches that can cause realistic responses to emerge without being forced into a model.

### 3.2. Adaptation

The ability of individuals to adapt is also a defining characteristic of CAS. In CAS, the term ‘adaptation’ is broadly defined as any behavior intended to improve an individual’s potential fitness. Systems of artificial agents generally become more interesting and lifelike as the ability of

agents to adapt increases. Models of very simple agents can display emergent system-level responses but are not capable of solving complex problems. On the other hand, the most powerful CAS models have highly adaptive agents like the genetic computer algorithms (Holland, 1995). The agents in these models can learn surprisingly difficult tasks, to the extent that they are now commonly used to solve complex engineering optimization problems.

Many biologists equate adaptation with genetic evolution, and it does not seem appropriate to include evolution in IBMs designed for environmental management. However, when we use a broad definition of adaptation as any change that improves potential fitness, we realize there are actually many kinds of adaptation used by organisms over a wide range of spatial and temporal scales. Using vertebrate animals as an example (Table 1), sub-evolutionary adaptations range from changes in behavior (e.g. feeding vs. hiding) at time scales sometimes less than a minute (Tinbergen, 1951) to changes in geographic range and

Table 1

Adaptation considerations for individual-based animal models, with ‘adaptation’ broadly defined as any behavior intended to increase potential fitness

Time scale	What adapts	Mechanisms of adaptation	Drivers of adaptation
Seconds–minutes	Behavior	Expression of innate short-term behaviors	Fear, hunger, aggression
Hours–days	Habitat choice	Movement	Spatial and temporal variation in food availability and risks, often due to competition, weather
	Knowledge of environment	Exploration	
Seasons–years	Life history state	Ontogeny, innate strategy selection behaviors	Animal size, energy reserves, reproductive status, experience
	Learned behaviors	Learning	
Generations	Geographic range	Exploration	Environmental change, competition, chance
	Life history	Phenotypic plasticity	
	Innate behaviors	Phenotypic plasticity	
Evolutionary time	Physiology	Genetic evolution	Selective pressures, genetic variability and mutation
	Innate behaviors		

life history characteristics over generations (Quinn and Adams, 1996).

Determining the characteristics of model individuals that should be adaptive (using the broad CAS definition), the mechanisms of adaptation, and the processes that adaptation responds to is an exercise that almost certainly will help focus and improve the design of an IBM. These decisions should be a function of the model's spatial and temporal scales, so designing a model's approach to adaptation should go hand-in-hand with designing its scales. A model of how a population responds to an impact in the short term should include adaptations that occur over short time scales (e.g. changes in habitat selection); a model of longer-term responses may consider adaptations like changes in geographic range and innate life history characteristics (Huse and Giske, 1998).

### 3.3. *Fitness and strategy*

Artificial complex systems that are powerful and lifelike in solving problems use fitness-seeking behavior by the individual agents (Holland, 1995, 1998). An important example class of models is the genetic algorithms, in which sets of behavior-defining rules evolve to increase their fitness at solving a particular problem. This approach requires specific and useful definitions of fitness: the ability of individuals to adapt and compete successfully is very dependent on a fitness measure that is clearly defined and meaningful. The definition of fitness provided in the model is critical because it defines the problem that the model's individuals then seek to solve; defining the problem incorrectly or incompletely will hamper the success of individuals and cause a model's results to seem unrealistic.

'Strategies' can arise in complex systems when agents learn that they can be more successful by switching their approach to seeking fitness. Holland (1998) describes the adaptive checkers-playing model of Samuel (1959), in which software agents improve their ability to beat opponents by switching among alternative functions for evaluating the expected success of potential moves.

One of the least controversial concepts in ecology is that organisms display behaviors that improve their potential fitness, where fitness is the individual's contribution to next generation's gene pool. The main problem that organisms seek to solve is to survive until they can reproduce and then to reproduce successfully. How an individual's potential fitness is represented in an IBM is often a key model design issue.

Most IBMs use some kind of fitness-seeking behavior, typically as part of a key decision-making process. For example, many models simulate habitat selection by individuals; the decision of whether to move and the selection among habitat patches are based on some measure of the animal's potential fitness at a patch. The fitness-seeking approach typically involves defining the fitness measure and making assumptions about how the organism evaluates the measure (e.g. what fitness-related information it does and does not know). The approach also requires modeling how decisions are based on the fitness measure, e.g. by: (1) picking the alternative that maximizes the fitness measure; (2) responding to a decline in the measure; (3) using simple heuristics (Gigerenzer et al., 1999); or (4) using neural nets to simulate adaptive, innate, behaviors (Huse et al., 1999). It should be noted that using fitness seeking in an IBM does not necessarily assume that the organisms actually conduct the often complicated calculations needed to evaluate fitness; it instead assumes that the fitness-seeking algorithm is a useful representation of an organism's actual decision-making behavior. The organism may actually make decisions using innate behaviors tuned by evolution, but such behaviors may be represented well by a model that assumes the organism evaluates and seeks potential fitness.

Models using fitness-seeking to make decisions have varied in the completeness of the measure used to represent potential fitness. Some models have based decisions on incomplete measures of potential fitness, such as selecting habitat considering only the amount of forage (Abbott et al., 1997) or the number of competing individuals (Clark and Rose, 1997) at a site. Other models have based decisions on measures more directly and completely describing key components of

fitness like expected survival and reproductive potential (Bull et al., 1996; Grand, 1999; Railsback et al., 1999).

Models in which organisms seek to maximize an indirect or incomplete measure of fitness may not produce realistic responses consistently. Telling animals to select habitat by choosing the site with maximum forage available, for example, implicitly assumes that forage availability is the only important factor driving potential fitness and that such other factors as predation risk, competition for the available forage, and the animals' energy reserves and reproductive state are never important to fitness potential. Such assumptions may be appropriate in some cases, but should be explicitly stated and justified.

The effects of using indirect measures of fitness potential in an IBM were examined by Railsback and Harvey (In prep.), who compared the ability of three fitness measures to reproduce realistic patterns of habitat selection in stream salmonids. Railsback and Harvey (In prep.) also compared survival and growth in a stream trout population predicted in simulations using the three fitness measures. This experiment used an IBM in which trout selected habitat to maximize either: (1) instantaneous net energy intake; (2) instantaneous survival probability; or (3) expected probability of surviving and growing to reproductive size over the next 90 days, as defined by Railsback et al. (1999). This experiment showed that using incomplete indicators of fitness like instantaneous energy intake or survival probability to model decision making sometimes produced unrealistic habitat selection behavior by individuals, and produced lower population-level survival and growth compared to the more direct fitness measure representing probability of survival and reproduction. (In general, fish maximizing instantaneous energy intake took unnecessary risks and suffered high predation rates; fish maximizing instantaneous survival probability neglected food intake and starved. The third fitness measure consistently produced good choices between food intake and risks over a wide range of conditions.)

For simulation of fitness-seeking decision making, designing an appropriate fitness measure can be a two step process. The first step is to deter-

mine the problem that the real animals are trying to solve and decide how much of this problem to include in the model. At least for full life cycle models, future survival and reproduction are likely an appropriate basis of fitness potential; the modeller's task becomes determining what processes driving expected survival and reproduction are important enough to be included in the model. Candidate drivers of fitness include: (1) net energy intake, as determined by such factors as food availability, feeding success, and energy costs as these factors vary with time, space, and competition; (2) mortality risks and their variation over time and space; and (3) physiological limitations. The second step is to design a mathematical representation of how expected fitness depends on the factors determined to drive fitness in reality. We have found the Unified Foraging Theory (below, Section 3.4), combined with an appropriate model of prediction (below, Section 3.5), to be a productive framework for developing fitness measures (Railsback et al., 1999).

The most appropriate measure used to represent fitness in an IBM may change with the state of an individual. Surviving and growing to reproductive size may be an appropriate measure for organisms in pre-reproductive life stages, but not for individuals that have attained reproductive size. Within a reproductive cycle, fitness may be dominated by successful completion of reproduction; and between reproductive cycles the most important component of fitness may be survival to, and acquisition of energy reserves for, the next cycle. Designing fitness measures that change with an individual's state is directly analogous to the CAS concept of strategy. For many IBMs it may be appropriate to design several fitness measures and rules for how individuals switch among them. The conceptual model of Thorpe et al. (1998), for example, lays out a strategy for how fitness measures change for salmon as they progress through their life cycle.

### 3.4. State-based responses

The agents in even the simplest CAS models have responses that are state-dependent: what the agents do in response to external stimulus de-

depends on the agent's current state. Examples include cellular automata, the behavior of which consists of changes in state in response to the agent's own state and that of its neighbors (Burks, 1970; Waldrop, 1992), and simple biochemical reaction systems (Winfree, 1987). Strategy selection among alternative fitness measures in a checkers-playing model described by Holland (1998) is also a state-based decision.

IBMs typically model the state of the individuals (e.g. their weight, length or height, and often some measure of energy reserves) and the outcome of model processes can vary with state (e.g. mortality may be more likely when size or energy reserves are small). However, state-based decision rules, where the decision rule an individual uses to respond to an external stimuli is a function of its current state, are rare in IBMs. For example, the trout model of Clark and Rose (1997) and the deer model of Abbott et al. (1997) have movement rules causing animals to select new habitat when food intake rate falls below a threshold. Although this threshold varies with animal size, the movement decision rule does not depend on current energy reserves. However, it seems unlikely that a real animal with ample fat reserves would always make the same choice between food intake and predation risks as a starving one.

One explanation of why IBMs rarely use state-based decision-making is that many models follow the early optimal foraging literature, which also neglected the effects of an animal's state. Foraging models that simply assume animals select habitat to maximize net energy intake or minimize the ratio of mortality risk to intake (Gilliam and Fraser, 1987) neglect how the relative fitness provided by these strategies depends on an animal's current energy reserves.

Newer approaches to foraging theory provide a useful conceptual framework for modelling state-based responses by individual animals. Our approach to modelling fitness-based decision making (Railsback et al., 1999) is adapted from the Unified Foraging Theory (UFT; Mangel and Clark, 1986; see Section 3.5 below). The UFT assumes that animals make choices over time to maximize their probability of surviving to, and having energy reserves for, future reproduction.

These choices depend on the animals' current energy reserve state. The related approach of Thorpe et al. (1998) makes state-based changes in the fitness measure used for key decisions. One of the reasons realistic habitat selection patterns emerge from the stream trout model discussed above (Section 3.1) is that the preferred tradeoff between mortality risk and food intake varies with the fish's current energy reserves. In this model, trout with low reserves are at risk of starvation so they maximize their expected fitness by selecting habitat with higher food intake even if other risks are higher; animals with ample energy stores put greater emphasis on habitat with low mortality risks.

### 3.5. Prediction

The ability to anticipate the outcome of alternative actions is critical to intelligent behavior in CAS models. Models in which agents learn to play games like checkers and chess are good examples: the agents learn to anticipate the consequences of possible game moves as a way of selecting good moves (Holland, 1998). However, prediction is key to even simple CAS models and biological systems. Holland (1995) discusses prediction using the framework of internal models that organisms use to anticipate outcomes. 'Tacit' internal models prescribe certain actions on the basis of implicit predictions that can be so simple that they are often not recognized as predictions. Holland provides the example of a bacterium that swims in a sugar gradient toward higher concentrations; the implicit prediction is that more food lies in the direction of increasing concentrations. 'Overt' internal models provide more explicit predictions of decision consequences using such information as internal maps of known habitat and known relations between habitat characteristics and mortality risks or food intake. An example use of overt models is the ability of some animals to make relatively consistent and predictable choices among habitats varying in risk and food intake (Grand and Dill, 1997); this behavior displays prediction of how potential fitness varies with habitat characteristics. In CAS models, explicit predictions are often conducted using the

'lookahead' approach, in which the expected consequences of alternative actions are forecast, so the approach most likely to be successful can be identified. The ability to anticipate the consequences of alternative responses is essential for successful adaptation, and it is clear that even the simplest organisms use tacit and perhaps overt internal models for prediction.

Including prediction in models of behavior does not necessarily mean assuming organisms have crystal balls or are capable of conducting complex lookahead computations. It seems very reasonable to assume instincts and physiological processes have evolved to provide organisms with approximate ways to anticipate future consequences of their behavior. For example, an animal trying to maximize its probability of survival while considering only instantaneous consequences would merely hide; it would not consider the possibility of starvation because starvation is not an immediate risk. However, we instinctively know that hiding is not a sustainable behavior because its future consequence will be starvation. In fact, hunger may be a physiological reminder that feeding, while not always an appropriate behavior (e.g. when predators are present), should not be long neglected. Hunger occurs long before energy reserves reach dangerous levels, so hunger can be viewed as a reminder of the future consequences of not feeding.

Modelling foraging and behavior almost always involves some level of prediction, but IBMs rarely use any form of prediction other than simple, implicit, and often unstated models. For example, in the trout models of Clark and Rose (1997), Van Winkle et al. (1998) fish move only after they have experienced a downward trend in fitness potential at their current habitat (an approach adopted from the model of Bernstein et al., 1988). The implicit predictions in these models are that the downward trend will continue and that fitness potential is more likely to improve if the animal moves. Behavior in many IBMs is modeled as a reactive, not overtly predictive, process: organisms make choices considering only current conditions, for example by maximizing instantaneous food intake.

The UFT and related methods described by Mangel and Clark (1986), Clark and Mangel (2000) assume that animals select among known foraging habitats to maximize their expected fitness over some future time period, a process that requires overt prediction. These dynamic modelling methods are not directly applicable to IBMs because they assume that habitat is static, whereas IBMs typically include habitat dynamics. In addition, competition for resources can cause resource availability to be dynamic even if other habitat characteristics are static. An animal cannot be assumed to optimize its habitat choices over time unless it makes some prediction of future resource availability. We adapted the UFT approach to an IBM with dynamic habitat by giving animals the simplest possible way to predict future resource availability: an animal assumes that future food intake and mortality risks over some decision time horizon will remain the same as they are at the time the animal makes its decision (Railsback et al., 1999). On each model time step, the animal uses this simplistic prediction of resource availability in a lookahead procedure to predict its probability of surviving and reaching reproductive size over the time horizon in each alternative habitat. Even this simple model of prediction produces more realistic behavior and higher fitness than do 'reactive' habitat selection approaches (Section 3.3). Bull et al. (1996), Grand (1999) use similar approaches, modelling animal decisions by assuming the individuals look ahead at their fitness potential over a future period.

It appears reasonable for IBMs to assume organisms have some ability to anticipate the future consequences to their fitness of their current actions. This ability allows modellers to use the state-based dynamic foraging approaches similar to UFT. The fitness advantages to an organism of basing decisions on long-term consequences of its actions, instead of reacting to immediate conditions, are high (Mangel and Clark, 1986; Railsback and Harvey, *In prep.*). It seems unlikely that organisms could be evolutionarily successful without this ability. Consequently, modellers need to carefully consider what ability to predict (and base decisions upon) future consequences of their decisions is appropriate in an IBM.

Uncertainty in organisms' predictions, and its consequences, is an unexplored and potentially interesting area for modelling research. Organisms certainly are limited in their predictive abilities and in some cases may suffer from having these abilities subverted. For example, trout raised to adult size in hatcheries have been observed to display inappropriate behavior and suffer rapid mortality when stocked into streams. Such mortality was modeled in the IBM of Van Winkle et al. (1998) by imposing a separate, high mortality factor for hatchery trout. I expect high mortality would also emerge automatically from a model in which hatchery trout use their hatchery experience as the basis for predicting consequences of habitat choices in a stream. If these fish predict, on the basis of their hatchery experience, that food availability is high in pools that resemble hatchery tanks and that mortality risks are generally negligible, their habitat choices in streams will be very poor.

### 3.6. Computer simulation

The vast majority of CAS research is conducted with computer simulation. As a result, the CAS community has developed a base of computer simulation expertise and tools that can greatly benefit IBM developers. The primary lesson from CAS is that IBMs, like CAS models, are so closely tied to their software implementation that computer science issues cannot be separated from other modelling issues. More than for conventional ecological models, how IBMs are implemented in software affects model results, our perception and understanding of model results, and our ability to do science.

The one product of CAS research that has been of most direct benefit to my colleagues and me is the *Swarm* simulation system, a software toolbox for individual-based simulation developed at the Santa Fe Institute (Minar et al., 1996; see also [www.swarm.org](http://www.swarm.org)). Interactions with *Swarm*'s developers and user community have allowed us to identify several key computer science issues for individual-based modelling.

One of the most important lessons about computer simulation that CAS researchers have

learned is the importance of user interfaces. Holland (1995) uses analogies to flight simulators and computer games like *SimCity* (Wright, 1989) to illustrate the importance of a graphical user interface for allowing modellers to understand models and determine when they do and do not produce realistic results.

IBMs are essentially untestable if the patterns of individual behavior cannot be observed. Observer capabilities like animation windows and the ability to check (and sometimes alter) the state of individuals during simulations are invaluable for testing and understanding IBMs. These tools may reduce the speed at which computer simulations execute, but they vastly increase the rate at which we can do science with IBMs. During development of all of our models, there have been instances where the animation window made it immediately apparent to us that our model had a programming error, an input data error, or a poor model assumption. These errors were often subtle and unlikely to have been detected without the animation window, yet had major effects on model results. This experience makes me doubt that many IBMs that lack such observer tools are sufficiently error-free to be used for research or management applications. On the other hand, when a model is working well the realistic behavior patterns displayed on the animation window are very powerful for building belief and interest in a model.

A second lesson from the CAS community (but also raised by Bart, 1995) is the importance of fully specifying models. Even small details of an IBM's formulation or computer implementation can have significant effects on model results; such details include choice of numerical methods, the order in which events are scheduled, and seemingly minor assumptions. For example, I was unaware, until starting to use *Swarm*, that many software platforms (programming languages, spreadsheets, etc.) include simplistic random number generators that have cycles that can induce errors, so the choice of random number generator is an important part of the model specification. Documenting an IBM in full detail is essential to make the model and its results reproducible and therefore suitable for science.

The final important lesson is the critical importance of software quality control. Because CAS models and IBMs are expected to produce novel and complex results, errors due to poor assumptions, programming mistakes, or flawed input are easily mistaken for valid results. At the same time, the complexity of a typical IBM makes it virtually impossible to hand-check results with any completeness. Ignoring these issues makes it very likely that considerable investigator time and funding are wasted using flawed code, or that invalid results are promulgated as science. Appropriate quality control measures are available in the computer science literature and absolutely essential for making IBM research cost-effective and scientifically valid. Our experience clearly indicates that taking software quality management seriously from the start leads to much more rapid, and less expensive, progress with IBMs.

These computer tool issues appear to be rarely understood or addressed by individual-based modellers (Grimm, 1999; Grimm et al., 1999; Lorek and Sonnenschein, 1999). Very few IBMs that have been published or used for ecological management have been accompanied with full documentation of the model's assumptions and adequate software testing, or implemented in software that even allows the behavior of model individuals to be observed and tested. Progress in individual-based ecology, as in any science, is unlikely in the absence of adequate tools.

Two practices can make it relatively inexpensive and easy to address these computer issues. The first is for ecologists to use software professionals to help do their toolmaking, just as scientists in virtually all other fields use engineers and other professionals to build their tools. All the issues raised here are widely understood and commonly addressed in computer science. Ecologists working on IBMs must give computer science issues serious consideration, but they need not become computer scientists if are willing to work with software professionals. The second practice is to use existing software platforms like *Swarm*. (There are a number of other platforms potentially appropriate for IBMs.) Such tools can provide the necessary user interfaces at virtually no cost, simplify and speed the coding process,

reduce the potential for errors, and reduce the new documentation needed to fully specify the model (Lorek and Sonnenschein, 1999). One of the greatest benefits to me of using *Swarm* has been access to the vast body of complex system modelling expertise resident in its developers and users.

#### 4. Conclusions

Individual-based modelling has important advantages as an approach for understanding and predicting ecological systems; primary among these advantages is the potential to avoid the unrealistic simplifying assumptions inherent in conventional, differential equation-based models (Huston et al., 1988). However, before these advantages can be realized modellers must learn how to build IBMs that realistically portray the individual- and system-level responses of natural populations. A set of approaches that have been demonstrated capable of producing realistic IBMs has yet to emerge and, in fact, there is little literature testing and comparing conceptual approaches for IBMs. I suggest that conventional ecological models persist not because they are fundamentally superior to complex systems approaches and IBMs, but in large part because their calculus-based conceptual framework is powerful and noncontroversial.

The past 10 years have shown that an ad hoc approach to IBMs is not productive. The study of CAS is too new to provide a detailed roadmap for individual-based modelling, partly because ecosystems are among the most complex systems known. However, by studying how complex and lifelike behaviors and dynamics arise in simplified systems CAS researchers have developed some key concepts that ecological modellers should consider. I propose the following as a list of concepts, identified as important in CAS, that should be addressed in designing IBMs. These concepts are intended to apply to IBMs in general, not just to models of animals or of any particular ecological issues.

#### 4.1. Emergence

What individual behaviors and population dynamics should emerge from the model's mechanistic representation of key processes? What other responses are appropriate to impose on the model as empirical relations? The consequences of these choices to the model's intended uses should be explicitly considered. Identifying traits of individuals and their habitat that produce realistic emergent responses is a fundamental modelling issue.

#### 4.2. Adaptation

Given the model's temporal and spatial scales and resolution, what adaptive processes should individuals be assumed to use? By what mechanisms do individuals adapt in response to what environmental forces?

#### 4.3. Fitness and strategy

If decision making by model individuals is based on fitness seeking, what measures of fitness are appropriate as the decision basis? Should fitness measures change with life history stage or other states?

#### 4.4. State-based responses

How should decision processes depend on an individual's state? Should decisions depend on an individual's size, energy reserves, or life history stage?

#### 4.5. Prediction

What are realistic assumptions about how organisms anticipate and consider future consequences in making decisions? Assuming that organisms base decisions only on immediate consequences, or in reaction to current or past events, appears unlikely to produce realistic behavior simulations.

#### 4.6. Computer implementation

What user interfaces are necessary to observe

the behavior of individuals, thereby making an IBM testable? How will the model's full design, including computer implementation details, be specified and documented so it is reproducible? What software testing methods are appropriate? Taking advantage of high-level modelling platforms and the expertise of software professionals helps make computer implementation adequate and cost-effective.

Consistently addressing these concepts should help make the design of IBMs less ad hoc and reduce the formulation and implementation problems that have limited the success of this important technology. These concepts can also provide a framework for IBM research and development: designing and testing ways to implement these concepts could focus research in ways that lead to established approaches for individual-based ecological modelling.

#### Acknowledgements

This research was sponsored by EPRI, Electric Power Research Institute Inc. under agreement EP-P1149/C433 with Lang, Railsback and Assoc., and by the Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture. I thank Geir Huse, Volker Grimm, and Peggy Wilzbach for valuable comments; my colleagues affiliated with Humboldt State University and Oak Ridge National Laboratory that participated in the modelling projects discussed here; and the *Swarm* development team and user community for providing the environment that stimulated these ideas.

#### References

- Abbott, C.A., Berry, M.W., Comiskey, E.J., Gross, L.J., Luh, H.-K., 1997. Parallel individual-based modeling of Everglades deer ecology. *IEEE Comp. Sci. Eng.* 4, 60–72.
- Auyang, S.Y., 1998. *Foundations of Complex-System Theories in Economics, Evolutionary Biology, and Statistical Physics*. Cambridge University Press, New York, p. 404.
- Bart, J., 1995. Acceptance criteria for using individual-based models to make management decisions. *Ecol. Appl.* 5, 411–420.

- Bernstein, C., Kacelnik, A., Krebs, J.R., 1988. Individual decisions and the distribution of predators in a patchy environment. *J. Anim. Ecol.* 57, 1007–1026.
- Booth, G., 1997. Gecko: a continuous 2D world for ecological modeling. *Artif. Life* 3, 147–163.
- Bull, C.D., Metcalfe, N.B., Mangel, M., 1996. Seasonal matching of foraging to anticipated energy requirements in anorexic juvenile salmon. *Proc. R. Soc. Lond. B* 263, 13–18.
- Burks, A.W. (Ed.), 1970. *Essays on Cellular Automata*. University of Illinois Press, Champaign-Urbana, Illinois.
- Clark, C.W., Mangel, M., 2000. *Dynamic State Variable Models in Ecology*. Oxford University Press, New York, p. 289.
- Clark, M.E., Rose, K.A., 1997. Individual-based model of stream-resident rainbow trout and brook char: model description, corroboration, and effects of sympatry and spawning season duration. *Ecol. Model.* 94, 157–175.
- Devreotes, P., 1989. Dictyostelium discoideum: a model system for cell-cell interactions in development. *Science* 245, 1054.
- Fama, E.F., 1991. Efficient capital markets II. *J. Finance* 46, 1575–1617.
- Folse, L.J., Packard, J.M., Grant, W.E., 1989. AI modelling of animal movements in a heterogeneous habitat. *Ecol. Model.* 46, 57–72.
- Forrest, S., 1990. Emergent computation: self-organizing, collective, and cooperative behavior in natural and artificial computing networks, introduction to the proceedings of the ninth annual CNLS conference. *Physica D* 42, 1–11.
- Gigerenzer, G., Todd, P.M., ABC Research Group, 1999. *Simple Heuristics that Make Us Smart*, Oxford University Press, New York.
- Gilliam, J.F., Fraser, D.F., 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68, 1856–1862.
- Goldspink, C., 2000. Modelling social systems as complex: towards a social simulation meta-model. *J. Artif. Society Social Sim.*, 3. <http://www.soc.surrey.ac.uk/JASSS/3/2/1.html>.
- Grand, T.C., 1999. Risk-taking behavior and the timing of life history events: consequences of body size and season. *Oikos* 85, 467–480.
- Grand, T.C., Dill, L.M., 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. *Behav. Ecol.* 8, 437–447.
- Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecol. Model.* 115, 129–148.
- Grimm, V., Frank, K., Jeltsch, F., Brandl, R., Uchmanski, J., Wissel, C., 1996. Pattern-oriented modelling in population ecology. *Sci. Total Environ.* 183, 151–166.
- Grimm, V., Wyszomirski, T., Aikman, D., Uchmanski, J., 1999. Individual-based modelling and ecological theory: synthesis of a workshop. *Ecol. Model.* 115, 275–282.
- Harvey, B.C., Nakamoto, R.J., White, J.L., 1999. Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout, (*Oncorhynchus clarki*) during fall and winter. *Can. J. Fish Aquat. Sci.* 56, 2161–2166.
- Hasler, A.D., Scholz, A.T., 1983. *Olfactory Imprinting and Homing in Salmon*. Springer-Verlag, New York, p. 134.
- Hilborn, R., Mangel, M., 1997. *The Ecological Detective*. Princeton University Press, Princeton, New Jersey, p. 315.
- Holland, J.H., 1995. *Hidden Order: How Adaptation Builds Complexity*. Perseus Books, Reading, Massachusetts, p. 185.
- Holland, J.H., 1998. *Emergence: From Chaos to Order*. Helix Books, Reading, Massachusetts, p. 258.
- Huse, G., Giske, J., 1998. Ecology in Mare Pentium: an individual based model for fish with adapted behavior. *Fish Res.* 37, 163–178.
- Huse, G., Strand, E., Giske, J., (1999). Implementing behavior in individual-based models using artificial neural networks and genetic algorithms. *Evol. Ecol.* 13, 469–483.
- Huston, M., DeAngelis, D., Post, W., 1988. New computer models unify ecological theory. *BioScience* 38, 682–691.
- Kaiser, H., 1979. The dynamics of populations as result of the properties of individual animals. *Fortschr. Zool.* 25, 109–136.
- Kauffman, S., 1995. *At Home in the Universe: The Search for the Laws of Self-Organization and Complexity*. Oxford University Press, New York, p. 321.
- Kohler, T.A., Kresl, J., Van West, C., Carr, E., Wilshusen, R.H., 1999. Be there then: a modeling approach to settlement determinants and spatial efficiency among late ancestral Pueblo populations of the Mesa Verde region, U.S. southwest. In: Kohler, T.A., Gumerman, G.J. (Eds.), *Dynamics in Human and Primate Societies*. Oxford University Press, New York.
- Kreft, J.-U., Booth, G., Wimpenny, J.W.T., 1998. BacSim, a simulator for individual-based modelling of bacterial colony growth. *Microbiology* 144, 3275–3287.
- Levin, S.A., 1999. *Fragile Dominion: Complexity and the Commons*. Helix Books, Reading, Massachusetts, p. 256.
- Lorek, H., Sonnenschein, M., 1999. Modelling and simulation software to support individual-based ecological modelling. *Ecol. Model.* 115, 199–216.
- Mangel, M., Clark, C.W., 1986. Toward a unified foraging theory. *Ecology* 67, 1127–1138.
- Mangel, M., Fiksen, Ø., Giske, J., In press. Logical, statistical, and theoretical models in natural resource management and research. In: Shenk T., Frankling A. (Eds.), *How to practice safe modeling: the interpretation and application of models in resource management*, Island Press, Washington, D.C.
- Minar, N., Burkhart, R., Langton, C., Askenazi, M., 1996. The *Swarm* simulation system: a toolkit for building multi-agent simulations. Santa Fe Institute Working Paper 96-06-042, Santa Fe, New Mexico.
- Murdoch, W.W., McCauley, E., Nisbet, R.M., Gurney, W.S.C., de Roos, A.M., 1992. Individual-based models: combining testability and generality. In: DeAngelis, D.L., Gross, L.J. (Eds.), *Individual-Based Models and Approaches in Ecology*. Chapman & Hall, New York, pp. 18–35.

- Nibbelink, N.P., Carpenter, S.R., 1998. Interlake variation in growth and size structure of bluegill (*Lepomis macrochirus*): inverse analysis of an individual-based model. *Can. J. Fish Aquat. Sci.* 55, 387–396.
- Nielsen, J.L., 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. *Trans. Am. Fish Soc.* 121, 617–634.
- Patten, B.C., Jørgensen, S.E. (Eds.), 1995. *Complex Ecology: The Part-Whole Relation in Ecosystems*. Prentice Hall, Englewood Cliffs, New Jersey, p. 705.
- Quinn, T.P., Adams, D.J., 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology* 77, 1151–1162.
- Railsback, S.F., In press. Getting ‘results’: the pattern-oriented approach to analyzing natural systems with individual-based models. *Nat. Res. Model.*
- Railsback, S.F., Harvey, B.C., In prep. Comparison of salmonid habitat selection objectives in an individual-based model. MS submitted to *Ecology*.
- Railsback, S.F., Lamberson, R.H., Harvey, B.C., Duffy, W.E., 1999. Movement rules for spatially explicit individual-based models of stream fish. *Ecol. Model.* 123, 73–89.
- Rose, K.A., 2000. Why are quantitative relationships between environmental quality and fish populations so elusive? *Ecol. Appl.* 10, 367–385.
- Samuel, A.L., 1959. Some studies in machine learning using the game of checkers. In: Feigenbaum, E.A., Feldman, J. (Eds.), *Computers and Thought*, 1963. McGraw-Hill, New York.
- Thorpe, J.E., Mangel, M., Metcalfe, N.B., Huntingford, F.A., 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evol. Ecol.* 12, 581–599.
- Thulke, H.-H., Grimm, V., Müller, M.S., Staubach, C., Tischendorf, L., Wissel, C., Jeltsch, F., 1999. From pattern to practice: a scaling-down strategy for spatially explicit modelling illustrated by the spread and control of rabies. *Ecol. Model.* 117, 179–202.
- Tinbergen, N., 1951. *The Study of Instinct*. Clarendon Press, Oxford.
- Uchmanski, J., 1999. What promotes persistence of a single population: an individual-based model. *Ecol. Model.* 115, 227–241.
- Uchmanski, J., 2000. Individual variability and population regulation: an individual-based model. *Oikos* 90, 541–550.
- Van Winkle, W., Jager, H.I., Railsback, S.F., Holcomb, B.D., Studley, T.K., Baldrige, J.E., 1998. Individual-based model of sympatric populations of brown and rainbow trout for instream flow assessment: model description and calibration. *Ecol. Model.* 110, 175–207.
- Waldrop, M.M., 1992. *Complexity: The Emerging Science at the Edge of Order and Chaos*. Simon & Schuster, New York, p. 380.
- Winfree, A.T., 1987. *When Time Breaks Down: The Three-Dimensional Dynamics of Electrochemical Waves and Cardiac Arrhythmias*. Princeton University Press, Princeton, New Jersey.
- Wright, W., 1989. *SimCity* (video game). Maxis Corporation, Orinda, California.