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Volker Grimm & Steven F. Railsback: Individual-based Modeling and Ecology

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Chapter One

Introduction

> The essence of the individual-based approach is the derivation of the properties of ecological systems from the properties of the individuals constituting these systems.
>
> —*Adam Łomnicki, 1992*

1.1 WHY INDIVIDUAL-BASED MODELING AND ECOLOGY?

Modeling attempts to capture the essence of a system well enough to address specific questions about the system. If the systems we deal with in ecology are populations, communities, and ecosystems, then why should ecological models be based on individuals? One obvious reason is that individuals are the building blocks of ecological systems. The properties and behavior of individuals determine the properties of the systems they compose. But this reason is not sufficient by itself. In physics, the properties of atoms and the way they interact with each other determine the properties of matter, yet most physics questions can be addressed without referring explicitly to atoms.

What is different in ecology? The answer is that in ecology, the individuals are not atoms but living organisms. Individual organisms have properties an atom does not have. Individuals grow and develop, changing in many ways over their life cycle. Individuals reproduce and die, typically persisting for much less time than the systems to which they belong. Because individuals need resources, they modify their environment. Individuals differ from each other, even within the same species and age, so each interacts with its environment in unique ways. Most important, individuals are *adaptive*: all that an individual does—grow, develop, acquire resources, reproduce, interact—depends on its internal and external environments. Individual organisms are adaptive because, in contrast to atoms, organisms have an objective, which is the great master plan of life: they must seek *fitness*, that is, attempt to pass their genes on to future generations. As products of evolution, individuals have traits allowing them to adapt to changes in themselves and their environment in ways that increase fitness.

Fitness-seeking adaptation occurs at the individual level, not (as far as we know) at higher levels. For example, individuals do not adapt their behavior with the objective of maximizing the persistence of their population. But, as ecologists, we are interested in such population-level properties as persistence, resilience, and patterns of abundance over space and time. None of these properties is just the sum of the properties of individuals. Instead, population-level properties *emerge* from the interactions of adaptive individuals with each other and with their environment. Each individual not only adapts to its physical and biotic environment but also makes up part of the biotic environment of other individuals. This circular causality created by adaptive behavior gives rise to emergent properties.

If individuals were not adaptive, or were all the same, or always did the same thing, ecological systems would be much simpler and easier to model. However, such systems would probably never persist for much longer than the lifetime of individuals, much less be resilient or develop distinctive patterns in space and time. Consider, for example, a population in which individuals are all the same, have the same rate of resource intake, and all reproduce at the same time. The logical consequence of this scenario (Uchmański and Grimm 1996) is that, of course, the population will grow exponentially until all resources are consumed and then cease to exist. Or consider a fish school as an example system with emergent properties (Huth and Wissel 1992, 1994; Camazine et al. 2001; section 6.2). The school's properties emerge from how individual fish move with respect to neighboring individuals. If the fish suddenly stopped adjusting to the movement of their neighbors, the school would immediately lose its coherence and cease to exist as a system.

Now, if ecologists are interested in system properties, and these properties emerge from adaptive behavior of individuals, then it becomes clear that understanding the relationship between emergent system properties and adaptive traits of individuals is fundamental to ecology (Levin 1999). Understanding this relationship is the very theme underlying our entire book: how we can use individual-based models (IBMs) to determine the interrelationships between individual traits and system dynamics?

But can we really understand the emergence of system-level properties? Ecological systems are, after all, complex. Even a population of conspecifics is complex because it consists of a multitude of autonomous, adaptive individuals. Communities and ecosystems are even more complex. If an IBM is complex enough to capture the essence of a natural system, is the IBM not as hard to understand as the real system? The answer is no—*if* we have an appropriate research program. But before we outline this program, which we refer to as "individual-based ecology," let us first look at three successful uses of individual-based models. Although these examples (which are described in more detail in chapter 6) address completely different systems and questions, they have common elements that play an important role in individual-based ecology.

1.2 LINKING INDIVIDUAL TRAITS AND SYSTEM COMPLEXITY: THREE EXAMPLES

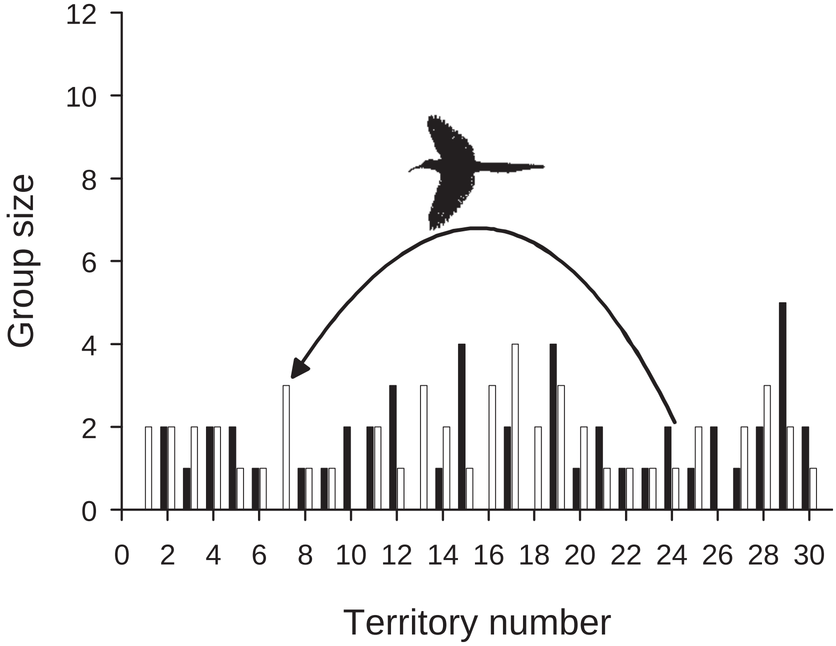
1.2.1 The Green Woodhoopoe Model

The green woodhoopoe (*Phoeniculus purpureus*) is a socially breeding bird of Africa (du Plessis 1992). The social groups live in territories where only the alpha couple reproduces. The subdominant birds, the "helpers," have two ways to achieve alpha status. Either they wait until they move up to the top of the group's social hierarchy, which may take years, or they undertake scouting forays beyond the borders of their territories to find free territories. Scouting forays are risky because predation, mainly due to raptors, is considerably higher while on a foray. Now the question is: how does a helper decide whether to undertake a scouting foray? We cannot ask the birds how they decide, of course, and we do not have enough data on individual birds and their decisions to answer these questions empirically.

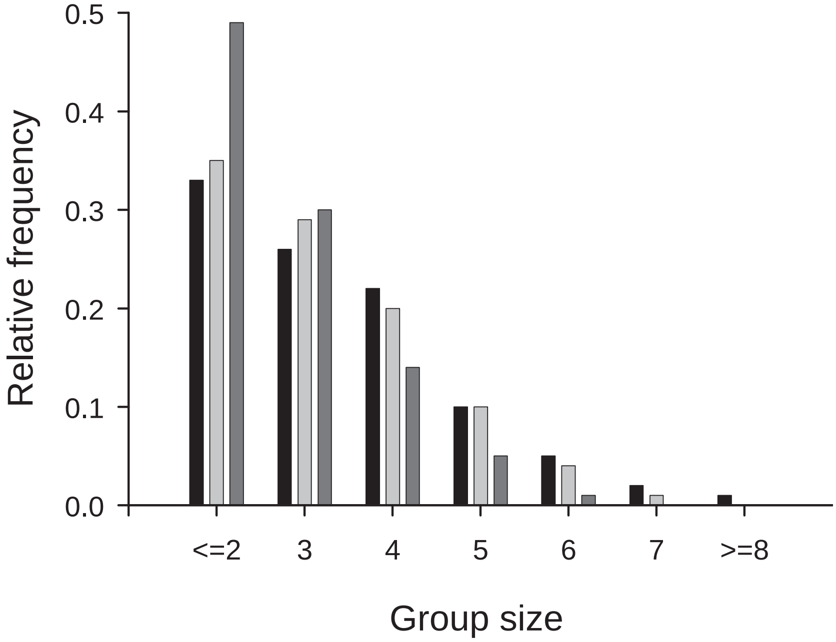
What we have, however, is a field study that compiled a group size distribution over more than ten years (du Plessis 1992). We can thus develop an IBM and test alternative theories of helper decisions by how well the theories reproduce the observed group size distribution (Neuert et al. 1995). These theories represent the internal model used by the birds themselves for seeking fitness. It turned out that a heuristic theory of the helpers' decisions, which takes into account age and social rank, caused the IBM to reproduce the group size distribution at the population level quite well (figure 1.1), whereas alternative theories assuming nonadaptive decisions (e.g. random decisions) did not. Then, after a sufficiently realistic theory of individual behavior was identified, questions addressing the population level could be asked—for example, on the significance of scouting distance to the spatial coherence of the population. It turned out that even very small basic propensities to undertake long-ranging scouting forays allow a continuous spatial distribution to emerge, whereas if the helpers only search for free alpha positions in neighboring territories the population falls apart (section 6.3.1; figure 6.5).

1.2.2 The Beech Forest Model

Without humans, large areas of Middle Europe would be covered by forests dominated by beech (*Fagus silvatica*). Foresters and conservation biologists are therefore keen to establish forests reserves that restore the spatiotemporal dynamics of natural beech forests and to modify silviculture to at least partly restore natural structures. But how large should such protected forests be? And how long would it take to reestablish natural spatiotemporal dynamics? What forces drive these dynamics? What would be practical indicators of naturalness in forest reserves and managed forests? Because of the large spatial


Group size
0
2
4
6
8
10
12
Territory number
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30

(a)


Relative frequency
0.0
0.1
0.2
0.3
0.4
0.5
Group size
<=2
3
4
5
6
7
>=8

(b)

and temporal scales involved, modeling is the only way to answer these questions. But how can we find a model structure that is simple enough to be practical while having the resolution to capture essential structures and processes?

What we can do to find the right resolution of the model is use patterns observed at the system level. For example, old-growth beech forests show a mosaic pattern of stands in different developmental phases (Remmert 1991; Wissel 1992a). The model must therefore be spatially explicit with resolution fine enough for the mosaic pattern to emerge. Another pattern is the characteristic vertical structures of the developmental stages (Leibundgut 1993; Korpel 1995). For example, the "optimal stage" is characterized by a closed canopy layer and almost no understory. The model thus has to have a vertical spatial dimension so that vertical structures can emerge (figure 1.2). Within this framework the behavior of individual trees can be described by empirical rules because foresters know quite well how individual growth and mortality depend on the local environment of a tree. Likewise, empirical information is available to define rules for the interaction of individuals in neighboring spatial units.

The model BEFORE (Neuert 1999; Neuert et al. 2001; Rademacher et al. 2001, 2004; section 6.8.3), which was constructed in this way, reproduced the mosaic and vertical patterns. It was so rich in structure and mechanism that it also produced independent predictions regarding aspects of the forest not considered at all during model development and testing. These predictions were about the age structure of the canopy, spatial aspects of this age structure, and the spatial distribution of very old and large trees. All these predictions were in good agreement with observations, considerably increasing the model's credibility. The use of multiple patterns to design the model obviously led to a model that was *structurally realistic*. This realism allowed the addition of model rules to track woody debris, which was not an original objective of the model. Again, the amount and spatial distribution of coarse woody debris in the model forest were in good agreement with observations in natural forest and old forest reserves (Rademacher & Winter 2003). Moreover, by analyzing hypothetical scenarios where, for example, no windfall occurred, it could be shown that storms and windfall have both desynchronizing (at larger scales) and synchronizing (at the local scale) effects on the spatiotemporal dynamics of beech forests. The model

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Figure 1.1 Individual decisions and population-level phenomena in the woodhoopoe IBM of Neuert et al. (1995). (a) Group size (*black*: male; *white*: female) in thirty linearly arranged territories. Subdominants decide whether to undertake long-distance scouting forays to find vacant alpha positions. (b) Observed group size distribution (*black*), and predicted distributions for the reference model (scouting decisions based on age and social rank; *light gray*); and a model with scouting decisions independent of age and status (*dark gray*). (After Neuert et al. 1995.)

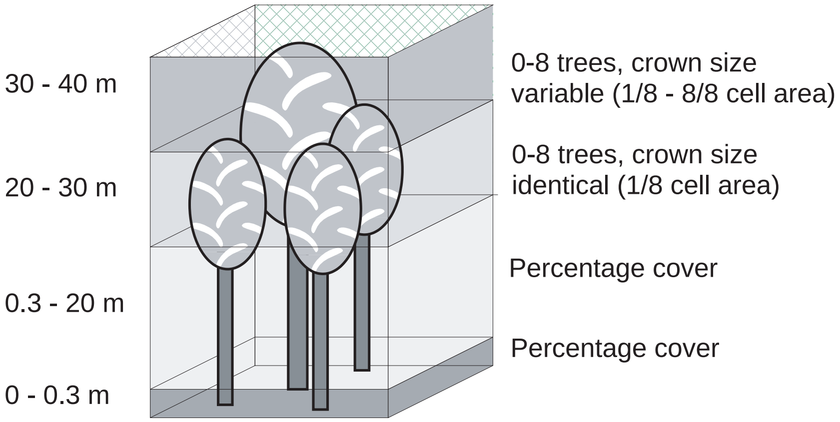

Figure 1.2 Vertical structure of the beech forest model BEFORE (Neuert 1999; Rademacher et al. 2001). (Modified from Rademacher et al. 2001.)

thus can be used for answering both applied (conservation, silviculture) and theoretical questions.

1.2.3 The Stream Trout Model

Models have been used to assess the effects of alternative river flow regimes on fish populations at hundreds of dams and water diversions. However, the approach most commonly used for this application, habitat selection modeling, has important limitations (Garshelis 2000; Railsback, Stauffer, and Harvey 2003). IBMs of stream fish have been developed as an alternative to habitat selection modeling (e.g., Van Winkle et al. 1998). These IBMs attempt to capture the important processes determining survival, growth, and reproduction of individual fish, and how these processes are affected by river flow. The trout literature, for example, shows that mortality risks and growth are nonlinear functions of habitat variables (depth, velocity, turbidity, etc.) and fish state (especially size), and that competition among trout resembles a size-based dominance hierarchy. River fish rapidly adapt to changes in habitat and competitive conditions by moving to different habitat, so modeling this adaptive behavior realistically is essential to understanding flow effects.

However, existing foraging theory could not explain the ability of trout to make good trade-offs between growth and risk in selecting habitat under a wide range of conditions. A new theory was developed from the assumption that fish select habitat to maximize the most basic element of fitness, the probability of surviving over a future period (Railsback et al. 1999). This survival probability considers both food intake and predation risk: if food intake is insufficient, the individual will starve over the future period, but if it feeds without regard for risk, it will likely be eaten. The new theory was tested by demonstrating that it could reproduce, in a trout IBM, a wide range of habitat selection patterns observed in real trout populations (Railsback and Harvey 2002).

Once its theory for how trout select habitat was tested, the IBM's ability to reproduce and explain population-level complexities was analyzed (Railsback et al. 2002). The IBM was found to reproduce system-level patterns observed in real trout including self-thinning relationships, "critical periods" of intense density-dependent mortality among juveniles, density-dependence in juvenile size, and effects of habitat complexity on population age structure. Further, the IBM suggested alternatives to the conventional theory behind these patterns (section 6.4.2).

In an example management application, the trout IBM was used to predict the population-level consequences of stream turbidity (Harvey and Railsback 2004). Individual-level laboratory studies have shown that turbidity (cloudiness of the water) reduces both food intake and predation risk. Whereas the population-level consequences of these two offsetting individual-level effects would be very difficult to evaluate empirically, they can be easily predicted using the IBM: over a wide range of parameter values, the negative effects of turbidity on growth outweighed the positive effects on risk.

1.3 INDIVIDUAL-BASED ECOLOGY

The preceding examples address different systems and problems, and the models differ considerably in structure and complexity. What they have in common, however, is the general method of formulating theories about the adaptive behavior of individuals and testing the theories by seeing how well they reproduce, in an IBM, patterns observed at the system level. The main focus may be more on the adaptive behavior of individuals, as in the woodhoopoe and stream trout examples, or on system-level properties, as in the beech forest example, but the general method of developing and using IBMs is the same.

This general method of using IBMs is a distinctly different way of thinking about ecology. We therefore have taken the risk of coining a new term, *individual-based ecology* (IBE), for the approach to studying and modeling ecological systems that this book is about. Classical theoretical ecology, which still has a profound effect on the practice of ecology, usually ignores individuals and their adaptive behavior. In contrast, in IBE higher organizational levels (populations, communities, ecosystems) are viewed as complex systems with properties that arise from the traits and interactions of their lower-level components. Instead of thinking about populations that have birth and death rates that depend only on population size, with IBE we think of systems of individuals whose growth, reproduction, and death is the outcome of adaptive behavior.

Instead of going in the field and only observing population density in various kinds of habitat, with IBE we also study the *processes* by which survival and growth of individuals are affected by habitat (and by other individuals) and how the individuals adapt.

The following are important characteristics of IBE. Many of these have more similarity to interdisciplinary complexity science (e.g., Auyang 1998; Axelrod 1997; Holland 1995, 1998) than to traditional ecology:

1. Systems are understood and modeled as collections of unique individuals. System properties and dynamics arise from the interactions of individuals with their environment and with each other.
2. Individual-based modeling is a primary tool for IBE because it allows us to study the relationship between adaptive behavior and emergent properties.
3. IBE is based on theory. These theories are models of *individual* behavior that are useful for understanding *system* dynamics. Theories are developed from both empirical and theoretical ecology and evaluated using a hypothesis-testing approach. The standard for accepting theories is how well they reproduce observations of real individuals and systems.
4. Observed patterns are a primary kind of information used to test theories and design models and studies. These patterns may be system-level patterns or patterns of individual behavior that arise from the individuals' interactions with the environment and other individuals.
5. Instead of being framed in the concepts of differential calculus, models are framed by complexity concepts such as emergence, adaptation, and fitness.
6. Models are implemented and solved using computer simulation. Software engineering, not differential calculus, is the primary skill needed to implement and "solve" models.
7. Field and laboratory studies are crucial for developing IBE theory. These studies suggest models of individual behavior and identify the patterns used to organize models and test theory.

We do not, of course, propose that IBE replace existing branches of ecology such as behavioral ecology or classical population ecology. We do not claim that IBE is the new "right" way to do ecology and that other approaches should be abandoned. Instead, IBE is a way to apply a variety of concepts, most of them already fundamental to ecology and other sciences, to kinds of problems that cannot be addressed by approaches that look only at individuals or only at populations. IBE is simply a new addition to the toolbox that ecologists can use to solve particular problems.

The IBE research program we develop in this book is based on but differs from earlier statements of the role of IBMs in ecology (e.g., Huston, DeAngelis, and Post 1988). These differences reflect the experience gained during the past twenty years or so, which has demonstrated both the potential and the specific problems of the individual-based approach. To understand how IBE deals with these problems, it is important to understand the problems and the reasons why they were not detected earlier. Therefore, in the following sections we give an overview of the development of the IBM approach, including the research programs outlined by the pioneers of IBM. We explain why it is important to clearly distinguish IBMs from the other modeling approaches which also consider individuals. Then, we briefly summarize the current status of individual-based modeling and list the most important challenges of the approach. Addressing these challenges is another major focus of this book.

1.4 EARLY IBMS AND THEIR RESEARCH PROGRAMS

Modeling the behavior of individuals and testing whether this behavior leads to realistic system-level properties is a natural idea. Therefore, IBMs were developed occasionally, and independently of each other, as soon as adequate computers were available (e.g., Newnham 1964; Kaiser 1974; Thompson et al. 1974; Myers 1976). Two early models were very influential and contributed significantly to the establishment of IBMs: the JABOWA forest model (Botkin et al. 1972) and the fish cohort growth model by DeAngelis, Cox, and Coutant (1980). The purpose of JABOWA was to model succession in mixed-species forests and thereby predict species composition. JABOWA was based on the notion that the interactions that drive forest dynamics are local. JABOWA gave rise to a full pedigree of related models (Liu and Ashton 1995, fig. 1; Shugart 1984; Botkin 1993) and probably is one of the most successful ecological simulation models ever developed. Reasons for the success of JABOWA include that it can be parameterized rather easily and its results are easily tested. (See section 6.7.5 for more details on JABOWA and other forest IBMs.)

The fish cohort model of DeAngelis, Cox, and Coutant (1980) is a similar success story. The model was able to predict accurately the outcome of laboratory experiments in which minute changes in the initial size distribution of the population led to completely different distributions at the end of the growth period. The reasons for this sensitivity to initial conditions were positive feedback mechanisms including asymmetric competition and cannibalism. As did JABOWA, the fish cohort model of DeAngelis et al. gave rise to a full family of fish cohort models (DeAngelis et al. 1990; Van Winkle, Rose, and Chambers 1993).

Interestingly, neither of these two influential models was presented as part of a larger program to develop individual-based modeling as an approach to ecology. Rather, the individual-based approach was chosen for pragmatic reasons: it would simply not have been possible to tackle these problems with classical approaches that ignore individual differences and local interactions. This pragmatic motivation of JABOWA and the fish cohort model is in contrast to the work of two other pioneers of the IBM approach, H. Kaiser and A. Łomnicki, whose attitude may be referred to as "paradigmatic" (Grimm 1999). They explicitly discussed the limitations of the classical ecological modeling paradigm and speculated about a new individual-based paradigm that could lead to fundamentally new insights.

Kaiser (1979) first constructed classical models to explain certain phenoma, for example, that the number of male dragonflies searching for mates along the shoreline of a lake was almost independent of the number of males foraging in the neighborhood of the lake. Kaiser then identified a number of limitations of these classical models: it was not possible "to trace the systems properties back to the behaviour of the individual animals"; the models contained parameters, for example, the arrival rate of male dragonflies at the shoreline, which have no direct biological meaning because "the dragonfly males have no means of observing the arrival rate"; and the parameters of the model were fit to one set of observations that reflected one certain environment, and there was no way to extend the model to situations beyond the original one. Kaiser concluded that the classical models did not offer much explanation of the processes determining population dynamics. In contrast, the IBMs developed by Kaiser used simple behavioral rules or physiological mechanisms for which empirical parameters were available. The *populations* had certain properties because *individuals* behaved in a certain way. This characteristic allowed the models to be extended—cautiously—to situations that were not observed in the field, such as longer or shorter shorelines and other temperatures.

The other paradigmatic pioneer, A. Łomnicki (1978, 1988), focused on the problem of why some individuals should leave a habitat of optimal quality and disperse to suboptimal habitat. Classical population models could not answer these questions because in classical models individuals are all the same. Within the framework of classical theory, the only solution to the problem of dispersal to suboptimal habitat was group selection: individuals behave suboptimally for the benefit of the population. Classical theory, Łomnicki argued, thus contradicts one of the most fundamental assumptions of evolutionary theory: that individuals (or their genes) are the units of natural selection, not groups of individuals. The only way to solve this dilemma is to construct models that include differences among individuals. As a central mechanism of population regulation, Łomnicki assumed that resources are unequally partitioned and that this inequality increases when resources become scarce (section 6.5.1). Ironically, the model used by Łomnicki to demonstrate regulation by unequal resource partitioning does not simulate individuals as discrete entities, but consists of two coupled difference equations. Although Łomnicki's attitude is strongly paradigmatic, claiming that classical theory leads ecology into a "blind alley," he still used the classical modeling approach.

Neither the work of Kaiser nor that of Łomnicki had a strong impact on the early development of the IBM approach. Kaiser received little attention because he published mainly in German. Łomnicki stuck to using analytical models, and his exclusive focus on resource partitioning and population regulation was too narrow to influence a larger array of modelers and ecologists.

The visionary article by Huston, DeAngelis, and Post (1988), "New computer models unify ecological theory," is widely regarded as having established the use of IBMs as a self-conscious discipline. Interestingly, this article does not discuss the paradigmatic notions of Kaiser and Łomnicki; Kaiser is ignored completely, and Łomnicki is only mentioned briefly. Instead, the article starts with the statement that "individual-based models allow ecological modelers to investigate types of questions that have been difficult or impossible to address using the [classical] state-variable approach" (p. 682). These questions include the significance of individual variability and local interactions among individuals. Huston et al. saw the main potential of IBMs as their ability to "integrate many different levels in the traditional hierarchy of ecological processes" (p. 682) because all ecological phenomena can eventually be traced back to the physiology, autecology, and behavior of individuals.

Today it is impressive to note how clearly all these pioneers saw both the pragmatic and paradigmatic potential of IBMs (see also the insightful early review of Hogeweg and Hesper 1990). On the other hand, these real pioneers cannot be blamed for not having foreseen all the challenges and limitations of the IBM approach so that these problems could have been recognized and tackled earlier. The first of these problems is to distinguish IBMs explicitly from other types of models.

1.5 WHAT MAKES A MODEL AN IBM?

Kaiser (1979) and Huston, DeAngelis, and Post (1988) defined IBMs as models that describe individuals as discrete and autonomous entities, but they did not precisely distinguish IBMs from classical models. The first and frequently cited volume about IBMs, entitled "Individual-based models and approaches in ecology" (DeAngelis and Gross 1992), also does not clearly delineate what an IBM is. The models considered in this volume range from IBMs as defined by Kaiser and Huston et al., to analytical models dealing with distributions of individual properties instead of discrete entities, to cellular automata that do not necessarily describe individuals at all. By the middle of the 1990s, the term "individual-based" had become so fuzzy that it became increasingly difficult to tell if IBMs really had the potential to unify ecological theory and to overcome the limitations of classical modeling approaches. Therefore, Uchmański and Grimm (1996) proposed four criteria that distinguish what we consider IBMs in this book, those reflecting the research programs of the IBM pioneers, from other more or less "individual-oriented" models that acknowledge the individual level in some way but still adhere mainly to the classical modeling paradigm.

The four criteria are: (1) the degree to which the complexity of the individual's life cycle is reflected in the model; (2) whether or not the dynamics of resources used by individuals are explicitly represented; (3) whether real or integer numbers are used to represent the size of a population; and (4) the extent to which variability among individuals of the same age is considered.

The degree to which the life cycle is reflected in a model (criterion 1) is important because individuals of most species change significantly in the course of their life: they need more and, often, different resources while they are growing; in different states of their development they interact with different biotic and abiotic elements of their environment; and individuals can adapt life history characteristics as they grow and develop, for example, growing or reproducing more slowly when resources are scarce or competition is high. IBMs thus have to consider growth and development in some way; otherwise they neglect essential aspects of the "ecology of individuals" (Uchmański and Grimm 1996).

The second criterion refers to resources exploited by individuals. Models that simply assume a constant carrying capacity for resources cannot be fully individual-based because they ignore the important, and often local, feedback between individuals and resources. Moreover, carrying capacity is typically a population-level concept, often used to describe density dependence in a population's growth rate. Such population-level concepts have little meaning at the individual level: individuals usually cannot know the overall density of their population but instead are affected by their local resources.

The third criterion is obvious: individuals are discrete so population size necessarily is an integer. However, sometimes classical models are made "individual-based" merely by rounding the real-number results to integer numbers. But the model's population dynamics are still fine-tuned using real numbers, whereas in real populations where individuals usually interact locally and only with a limited number of other individuals, this fine-tuning does not exist. Truly individual-based models are built using the mathematics of discrete events, not rates.

The fourth criterion distinguishes models using age, size, or stage distributions from IBMs. In distribution models, differences among individuals belonging to the same group (e.g., age-class) are ignored. In reality, however, even individuals of the same age, or size, may develop along different pathways so that after some time the variation among individuals within a class is comparable with the variation among class averages (Pfister and Stevens 2003). Neglecting this degree of freedom in population structure could mean ignoring important mechanisms determining population dynamics.

This classification scheme has been described as interfering "with the insightful process of comparing models at different levels of detail" (Bolker et al. 1997), but this was not the intent of its authors (Uchmański and Grimm 1997). Their objective was not to distinguish models as true and false, or useful and useless, but to provide classification criteria necessary to answer the question of whether IBMs can lead to a fundamentally new view of ecological systems and processes (Uchmański and Grimm 1996). This question cannot be answered unless IBMs are clearly delineated from other kinds of models, which we here refer to as "individual-oriented."

Of course, numerous models do not fulfill all of these four criteria but nevertheless provide important theoretical insights. Matrix models describing age- or stage-structured populations are powerful for determining the intrinsic rate of increase and the stable age or stage structure of exponentially growing populations (Caswell 2001). More sophisticated distribution models successfully describe laboratory populations of planktonic species (Dieckmann and Metz 1986), or patterns in fish communities (Claessen, de Roos, and Persson 2000). Models of predator-prey systems that describe individuals as discrete units having local interactions but no life cycles or variability can demonstrate the stabilizing effect of local interactions and the emergence of striking spatial patterns (de Roos, McCauley, and Wilson 1991; figure 1.3; see also Donalson and Nisbet 1999; section 6.6.1). All these models consider individuals to some extent but still refer to the framework of classical models and theory. They ask: what do we gain—compared with using classical, highly aggregated models—if we include, for example, the discreteness and local interactions of individuals (Durrett and Levin 1994)? But none of these "individual-oriented" models allows us to fully "trace the systems properties back to the behaviour of the individual animals" (Kaiser 1979, p. 116).

Individual-oriented models are, like classical models, indispensible, useful, and sometimes fascinating tools, but they should indeed be "separated" (Bolker et al. 1997) from IBMs. This separation is necessary if we are to compare the classical framework, which describes ecological systems as relatively simple and characterized by system-level state variables, to the view that ecological processes and systems emerge from the traits of adaptive individuals.

1.6 STATUS AND CHALLENGES OF THE INDIVIDUAL-BASED APPROACH

The individual-based approach is now firmly established in ecology. Hundreds of publications have been based on IBMs, prompting Grimm (1999) to review fifty IBMs of animal populations published in the decade after the paper of Huston, DeAngelis, and Post (1988). Earlier reviews of IBMs (DeAngelis et al. 1990; DeAngelis, Rose, and Huston 1994; Hogeweg and Hesper 1990) provide useful summaries of existing IBMs, but Grimm focused on the degree to which the vision that IBMs "unify ecological theory" (Huston, DeAngelis, and Post 1988) has been fulfilled. The conclusion of this review was rather sobering: although every model served its purposes and was thus

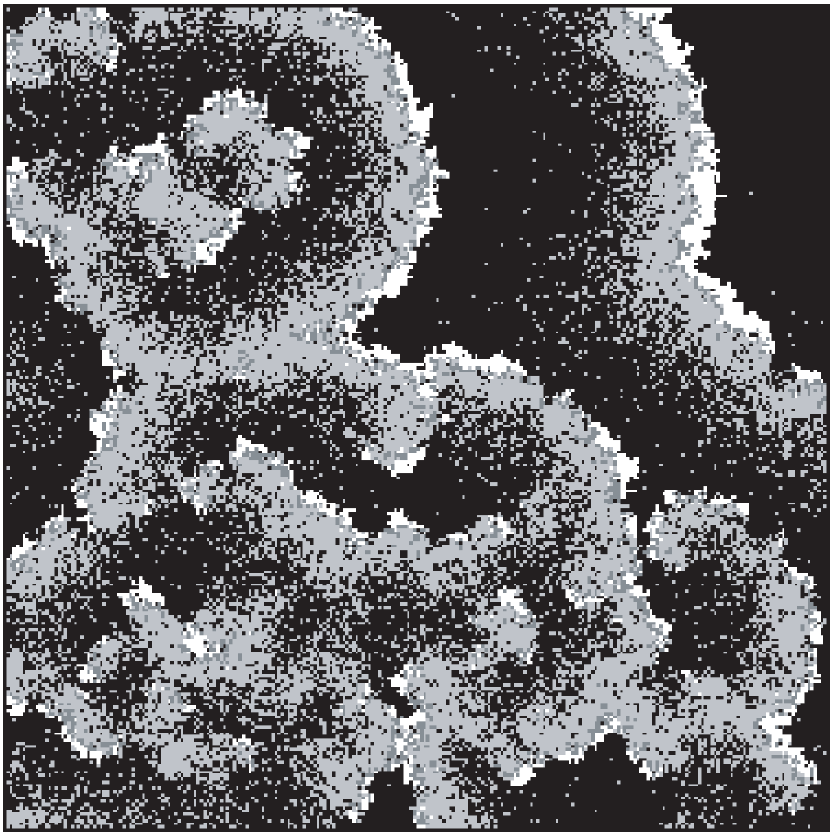

Figure 1.3 Spatial patterns produced by the model by de Roos, McCauley, and Wilson (1991) of an artificial predator-prey system. The model world consists of 256 × 256 grid cells, which can be in the states empty (*black*), prey (*white*), predator (*gray*), or predator handling prey (*dark gray*). Predator individuals are just "points" that jump to neighbor cells and eat, if present, prey "points." (Figure produced using a program written by H. Hildenbrandt.)

useful, ecology as a whole seemed to have learned less from the individual-based approach than originally expected. The main reason for this conclusion was that few IBMs addressed general issues of theoretical population ecology like persistence, resilience, or regulation. Similarly, new theoretical issues like emergence (chapter 5) or self-organization were rarely discussed; IBM applications seemed driven more by pragmatic motivations then by paradigmatic ones. Grimm (1999) also concluded that most IBMs were: (1) developed for specific species with no attempt to generalize results; (2) rather complex, but lacking specific techniques to deal with this complexity; and (3) too elaborate to be described completely in a single paper, making communication of the model to the scientific community incomplete (note that both JABOWA and the fish cohort model of DeAngelis, Cox, and Coutant 1980, mentioned earlier as particularly influential IBMs, were each completely described in one report).

The pioneers' vision that IBMs would induce a paradigm shift and unify ecological theory has clearly not come true automatically. The promise of the individual-based approach still exists (as we will try to show in this book), but the experience gained in one and a half decades of individual-based modeling shows that two closely linked problems have been underestimated. First is the complexity of IBMs, which "imposes a heavy cost compared with the other model types" (DeAngelis et al. 1990, p. 585) in understanding, testability, data requirements, and generality (Murdoch et al. 1992). Second is the lack of a theoretical and conceptual framework for individual-based modeling, leading to the widespread use of ad hoc assumptions and preventing a more coherent development of the approach (Hogeweg and Hesper 1990).

Because IBMs deal with many entities, spatial scales, heterogeneities, and stochastic events, they are necessarily more complex than classical, analytically tractable models. Many IBMs are complex as indicated by such conventional measures as the number of variables, parameters, or rules in the model. However, even IBMs that are relatively simple by conventional measures can be complex in new ways, such as in the number of unique individuals; the number, type, and order of interactions among individuals; and the number of ways a model population can reach any particular state. This complexity, along with the lack of an overall theoretical framework for individual-based modeling, has resulted in the following challenges to the productive use of IBMs. (Do not panic! This book shows how to meet these challenges.)

Development. Developing IBMs is a challenge because much more of the complexity of the real world is acknowledged and not ignored a priori. Designing the model structure and resolution is a more time-consuming and complex task than when developing classical models, which are constrained to a coarser representation of reality.

Analysis and Understanding. The more complex a model, the more difficult it is to analyze and understand. Many theorists and modelers therefore assume that an increase in complexity inevitably reduces a model's potential to provide understanding. Critics of IBMs argue that complex models are as hard to understand as the real world and therefore of little use.

Communication. Classical models are easy to communicate because they are formulated in the common language of mathematics. IBMs, on the other hand, have essential characteristics that cannot be described by equations and parameters. As yet, we lack a common, concise language for communicating IBMs. Moreover, many IBMs are too big to describe completely in publications. Therefore, IBMs are often not fully open and available to the scientific community, which is probably the most serious threat to the credibility of the whole approach (Lorek and Sonnenschein 1999; Grimm 1999, 2002; Ford 2000).

Data Requirements. The more kinds of entities, scales, and events a model represents, the more parameters are needed. Sufficiently precise parameter values are, however, notoriously difficult to obtain in ecology. IBMs have therefore been criticized as being too "data hungry"—especially IBMs designed for specific, applied problems. For example, the usefulness of spatially explicit population models, many of which are individual-based, has been questioned because adequate parameter values are never available (Beissinger and Westphal 1998).

Uncertainty and Error Propagation. Data available to parameterize IBMs are likely to be uncertain. Thus, keeping the number of parameters low seems wiser because many uncertain parameters might combine to produce extremely high uncertainty in system-level results. This error propagation potential appears capable of rendering IBMs totally useless for solving applied problems and of limiting the testability of IBMs, yet this aspect has received very little investigation.

Generality. Classical models using population size as a state variable are considered most general because they ignore almost every aspect of real species and populations. As more details are included (e.g., adding age or stage structure, space, habitat dynamics, dispersal), models become less general. Each detail added to a model makes it more specific to a particular population. How, then, can IBMs be general or produce theory when they are highly detailed? It has even been argued that using IBMs necessarily means relinquishing the "holy grail" of general ecological theory (Judson 1994).

Lack of Standards. Classical theoretical ecology has a suite of standard models with known properties. These standard models serve as building blocks for all kinds of structured classical models. It is no longer necessary to explain or even to justify the use of these standards. If, for example, a model addressing synchronization of local population dynamics in different patches assumes that the local dynamics are described by the so-called Ricker equation, the assumption is familiar and noncontroversial. Using this standard assumption makes analysis, communication, and comparison to other similarly structured models easier. In contrast, most IBMs have been built from scratch, using ad hoc assumptions not guided by general concepts. The lack of standard, widely accepted building blocks makes individual-based modeling both inefficient and controversial. This lack also makes it difficult to compare models and develop theory. If two IBMs produce different results, it is much more difficult to explain and learn from the differences when the IBMs have different structures and use many nonstandard assumptions.

Many of these same challenges have limited the progress of individual-based (or "agent-based," the term used in fields other than ecology) approaches in other fields of science. A period of initial excitement and exploration (e.g., Waldrop 1992; Arthur 1994; Axelrod 1984, 1997) has not been followed by as much rapid progress as some undoubtedly expected. Our observations have been that agent-based modeling has not become a widespread, paradigm-altering tool even among scientists focused on complexity (although there are important and exciting exceptions to this generalization). Building and learning from the models, and producing results of general theoretical interest, have proved difficult.

1.7 CONCLUSIONS AND OUTLOOK

The individual-based approach is no longer new, being established as a distinct approach for more than ten years now and having intrigued ecologists for over twenty years. IBMs can address types of questions that cannot be addressed with classical models. From many IBMs of real and hypothetical systems, we have learned much about the ecological significance of local interactions, individual variability, and so on. However, the most notable result of our experience with IBMs so far may simply be an understanding of the approach's many challenges and fundamental differences from classical ecology. The potential of IBMs remains high yet largely unfulfilled. To see this potential realized in the future, it is now time to formulate strategies for coping with the challenges we have listed in the preceding section.

This book presents our reseach program for IBE, much of which concerns strategies for coping with the problems that have limited IBMs so far. These strategies, outlined here, are adapted from existing theory and practice in ecological and simulation modeling, analysis of complex systems, and software engineering.

Pattern-oriented Modeling. The term "IBM" contains not only the word "individual" but also the word "model." So far, methodological work on IBMs has focused too much on individuals and their significance and not enough on modeling. Perhaps the most decisive modeling issue is how to find the optimal level of complexity for an IBM. Using multiple patterns at different levels of ecological process ("pattern-oriented modeling") helps optimize model complexity, parameterize models, and make models testable and general.

Theory. In IBE, "theory" mainly concerns how to represent individual-level behavior in a way useful for explaining system-level processes. These theories could also be referred to as "models" or "assumptions," but referring to "theory" underlines the research program of IBE: to develop a general theoretical framework for describing individual behavior. The rationale of this program is that generality should be easier to achieve at the individual level than at aggregate levels because all individuals follow, as pointed out earlier, the same master plan: seeking fitness. Individuals must continually decide—in the literal or the more metaphorical sense—what to do next, and these decisions are based on the individual's internal models of the world. It seems reasonable to believe that individuals of many types have similar internal models and traits that are based on fitness seeking; and complexity science teaches us that individuals with identical adaptive traits but their own unique states, experiences, and environments can produce an infinite variety of system dynamics. Coherent and predictive theories of these traits will provide an important key to understanding ecological phenomena in general.

Design Concepts. Designing every element of a model requires decisions about variables, parameters, functional relationships, and the like; and if these decisions are not to be ad hoc, they must be based on a consistent set of concepts. Unfortunately, differential equations do not provide a useful conceptual framework for IBMs. Instead, a general conceptual framework for designing IBMs can be borrowed from the new discipline of Complex Adaptive Systems (CAS; Waldrop 1992; Holland 1995, 1998). Such concepts as emergence, adaptation, and prediction can provide an explicit basis for design decisions and reduce the need for ad hoc modeling decisions. These concepts also provide a common terminology for designing and describing IBMs.

Software Design and Implementation. Software development is inevitably a major part of an IBE project, and project success requires software that is well designed and thoroughly tested. Computer models are the primary tools of IBE and, as in any other science, the rate and nature of progress are highly dependent on the quality of the tools. Successful conduct of IBE often requires software expertise beyond the meager training ecologists now typically receive.

Simulation Experiments. We can only understand and learn from simulation models such as IBMs if we design and execute controlled simulation experiments. Thus, the art of analyzing IBMs is in designing experiments whose outcome can (at least partly) be predicted, and falsified, and to combine such experiments in a way that we get a comprehensive understanding of the key structures and processes of ecological systems. The ability of this experimental approach to produce new and general insights has been demonstrated in a number of studies.

Communication. The complexity of IBMs and newness of IBE makes scientific communication more important yet more challenging. Both models and software need full documentation, and often separate publications are required to describe an IBM and then its research or management applications. A model, or any scientific idea, is successful if it is memorized in total or part by peers who then use it in future work. Improving this "memetic fitness" (Blackmore 1999) of IBMs is critical to the success of IBMs and IBE.

Where will we be in another decade or two? We envision IBE being conducted by interdisciplinary teams having expertise in simulation modeling and complex systems science, software engineering, and the biology and ecology of the organisms and systems being studied. As in other kinds of ecology, toolboxes of standard IBE modeling practices, theory, software, and analysis methods will gradually be developed and refined as more models are designed and tested and more theory is developed. These toolboxes will allow us to build models rapidly and conduct analyses of many ecosystem dynamics and complexities that we currently cannot explain. IBE and more traditional approaches will continue to contribute to each other in many ways (e.g., see chapter 11). However, what will continue to set IBE apart is its goal not to simplify ecological complexity but to *understand* complexity and how it emerges from the adaptive traits of individuals.