Individual Based Models in Ecology:
An Evaluation, or How Not to Ruin a Good Thing

Joan Roughgarden
Professor Emerita, Dept. of Biology, Stanford University
Adjunct Professor, Hawai`i Institute of Marine Biology, U. of Hawai`i

Background: What are now increasingly called individual based models (IBMs) have been used in ecology since the 1970s when theoretical ecology began in earnest. The best known examples from that time include the forest computer simulation model (named JABOWA) of Daniel Botkin (Botkin et al 1972) and the computer simulation model of Donald DeAngelis (DeAngelis et al 1991) for a freshwater fish cohort. These were identified with the systems ecology school of theoretical ecology and the approach was anticipated to offer a unifying theoretical framework for ecology (Huston 1988), a goal whose possibility is still being debated (Roughgarden 2009, Vellend 2010). Since then hundreds of IBMs have been published in ecology. Moreover, IBMs are being actively developed in other disciplines, especially the social sciences, and dozens of software environments have been created to facilitate IBM research (Allen 2010, Borrill and Tesfatsion 2012). This talk reviews progress for IBMs in ecology, details several remaining difficulties, and suggests clarification where needed.

Provisional Definition: For now, an IBM is provisionally considered to be a computer simulation in discrete time steps for the creation, disappearance and movement of a finite collection of discrete interacting entities. The germination, growth and death of a collection of individual trees on a plot of ground, or the birth, growth and reproduction of a collection of individual fish in a pond are the classic examples.

Challenges Met: Grimm and Railsback (2005) detail seven "challenges" that IBMs have faced in ecology: long time needed to develop the model, difficulty in analyzing results, lack of common language to communicate model and results, requirement for too much data, uncertainty and error propagation, lack of generality, lack of standards. Ecological IBM modelers have faced these challenges head on. They have collectively proposed and implemented a protocol (called the "ODD protocol") for how a model is to be specified (Grimm et al 2006, 2010), and they have coalesced around a freely downloadable programming platform, NetLogo (Wilensky 1999, 2013), as a standard for developing and executing IBMs (Lytinen and Railsback 201, Railsback and Grimm 2011). Moreover, NetLogo can be embedded within Mathematica (Wolfram Research) thereby endowing the IBM modeling module with the statistical and analytical tools of Mathematica's powerful industry-standard mathematical programming environment. The steps by the ecological IBM modeling peer group go a long way toward resolving many,

but not all, of the reservations that have dogged IBMs since their inception. Here are some remaining problems.

Exclusionary Definitions: Despite their progress, ecological IBM modelers have also taken decisions that seem counter productive. They employ an unnecessarily exclusive definition of what counts as an IBM. Grimm and Railsback (2005), following Uchmanski and Grimm (1997), stipulate that to be considered an IBM in ecology, the model must satisfy four criteria:

1. Detail about each individual's life cycle must be present in the model, including the growth and development of each individual as it ages.
2. The dynamics of resources used by individuals must be explicitly represented - a "carrying capacity" cannot be used because it is supposedly a population-level concept and that cannot be known to an individual.
3. Integers and not real numbers must used to represent the size of a population-the model must feature discrete events and not refer to rates.
4. Variability must be allowed and must exist among individuals of the same age - environmental phenotypic variation, not heritable genetic variation, in as much as Grimm and Railsback (2005) consider evolutionary ecology as beyond the scope ecological IBMs.

Inconsistent Definitions: Grimm and Railsback (2005) acknowledge that these criteria rule out many models as IBMs. Notable among the excluded models are "predator-prey systems with individuals as discrete units with local interactions but no life cycles or variability among individuals". However, this criterion conflicts with standard practice in the wider IBM community. Wolfram's Mathematica website has a demonstration by Sayama (no date given) of a "real-time agent-based simulation of a predator-prey ecosystem" wherein rabbits run around in a square area and are chased by foxes. Castiglione (2006), in the Scholarpedia peer-reviewed open-access encyclopedia entry about agent-based modeling, also features a direct comparison of an an individual-based fox-rabbit model compared with the venerable Volterra predator/prey model that is formulated as pair of coupled non-linear differential equations. The fox-rabbit models proposed as examples of IBMs would nonetheless be ruled out as ecological IBMs by Grimm and Railsback even though they are offered precisely as illustrations of IBMs in the wider IBM literature.

Why So Restrictive? In acknowledging that their definition is restrictive, Grimm and Railsback (2005) refer to models that seem in some respect to be IBMish but are not true IBMs, as "individual-oriented". Why do Grimm and Railsback care so much about retaining their exclusionary definition? Because they are committed to the ideal that "IBMs can lead to a fundamentally new view of ecological systems and processes". They write that unlike true IBMs, "individually-oriented models do not allow us to fully trace the systems properties back to the behavior of the individual animals". The ecological IBM modelers regularly disparage the "classical framework" for describing ecological systems as "relatively simple and characterized by system-level state variables", vs "the IBM view that ecological processes and systems emerge from the

traits of adaptive individuals", and they view their exclusionary definition of an IBM as necessary to accomplish this aim. Let us consider then whether the restrictions are in fact necessary to attaining a "fundamentally new view of ecological systems."

"Individually Oriented" Models Are Sufficient: I now review two examples of models that are IBMish but do not satisfy Grimm and Railsback's (2005) criteria, and show that these do represent a fundamentally new approach to formulating ecological models.

(1) Optimal Size of an Optimal Forager: In 1995 I published a model for how a lizard could learn to forage optimally (Roughgarden, 1995). The model predicted the "optimal cutoff distance" such that all prey closer than this distance are taken and all prey beyond this distance are ignored. The optimal distance is that which
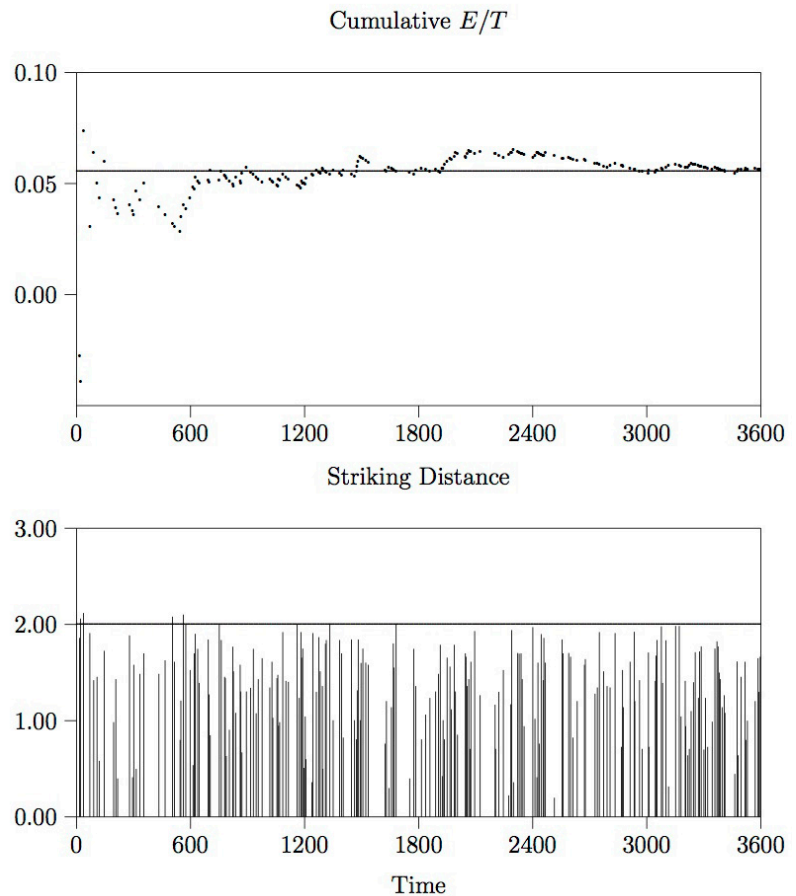
Cumulative E/T

Striking Distance

Figure 1.15: Top: Net energy gained per elapsed time in joules/s during one h of foraging, as noted after each prey capture. Expected yield from optimal home range shown as horizontal line. Bottom: Distance in m of successful strikes as function of time in s. Optimal cutoff radius shown as horizontal line. Insect length is 2.5 mm, prey flightiness coefficient is 1, abundance is 480 insects per m^2 per 12 h, lizard SVL is 45 mm, and lizard's memory extends to beginning of foraging period.

maximizes the lizard's rate of energy capture. A simple algorithm was exhibited that would allow a lizard to dynamically learn where the optimal cutoff was. The figure above illustrates the model using parameters estimated from field data for *Anolis* lizards in the Eastern Caribbean. The lower panel shows the optimal cutoff distance as a horizontal line. Prey are appearing randomly at distances from 0 to 3 m away from the lizard. Each vertical line represents a prey item that was chased and caught. Notice that vertical lines rarely cross the optimal cutoff, and those that do are principally at the beginning of the simulation when the lizard is still learning where the optimal cutoff distance is. The upper panel shows how the lizard's energy capture rate within a day approaches the optimal capture rate, shown as a horizontal line. The realized capture rate fluctuates initially reflecting the lizard making mistakes by chasing insects beyond the optimal cutoff distance or ignoring insects in front of the optimal cutoff distance. The existence and quantitative properties of the optimal cutoff distance were tested and confirmed in field studies of *Anolis* lizards on the island of Anguilla (Shafir and Roughgarden 1998).

Based on this model for the daily energy capture by a lizard, the daily growth rate of a lizard could be predicted. The next figure shows a scatter plot of lizards' daily growth increments from field data compared to that theoretically predicted assuming a lizard is an optimal forager. The open circles pertain to females and the closed circles to males. The theoretically predicted optimal growth rate is the solid curve. Notice the quantitative agreement between actual growth increments and that expected from optimal foraging theory. Females cease growing and drop off the curve when they have reached a length of about 45 mm and the males drop off the growth curve at about 60 mm in length. These sizes are typical of adults on those Eastern Caribbean islands with only one species of anole (the so-called solitary size).
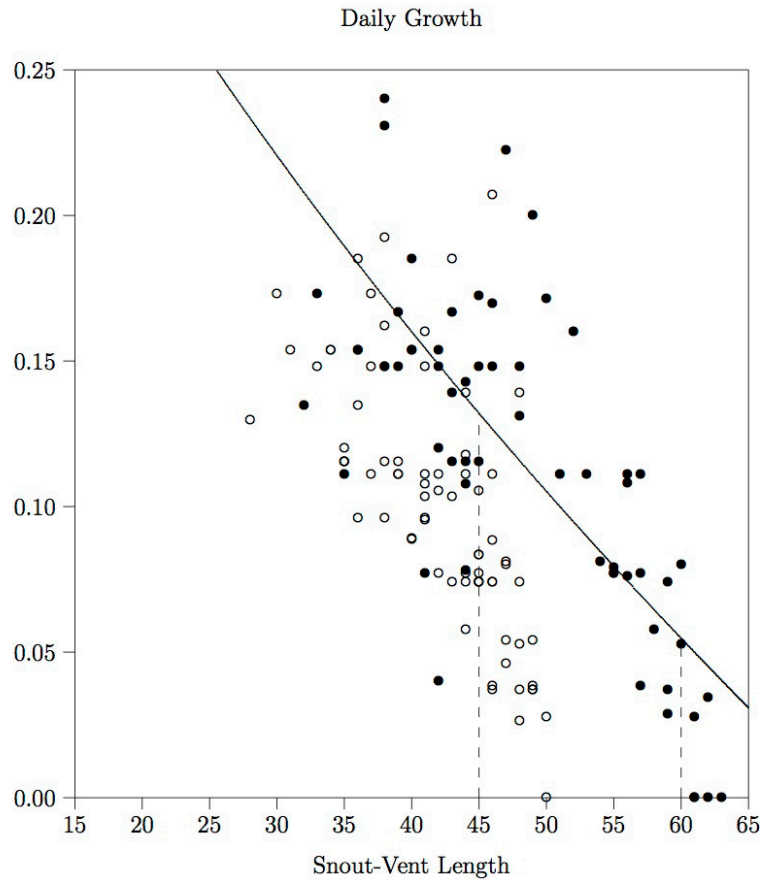
Daily Growth

Figure 1.22: Growth of *Anolis gingivinus* in mm/d for males (●) and females (○) in St. Martin from December 1980 to April 1981 as a function of a lizard's snout-vent length in mm. Solid descending curve is growth predicted from optimal foraging theory assuming 3.5 h foraging time per d and using the optimal foraging parameters of Figure 1.16. Vertical dashed lines are conjectured switches from growth to reproduction, for females at 45 mm and males at 60 mm.

The next task is to predict why the lizards stop growing at the sizes they do in order to begin reproduction at that time. To accomplish this, the optimal growth rate curve can be integrated through time to yield a predicted curve of how the size of a lizard changes as it ages as shown in the adjacent figure.

This theoretically predicted growth curve is then combined with field estimates of survivorship and with a maternity function predicted from the fecundity of an
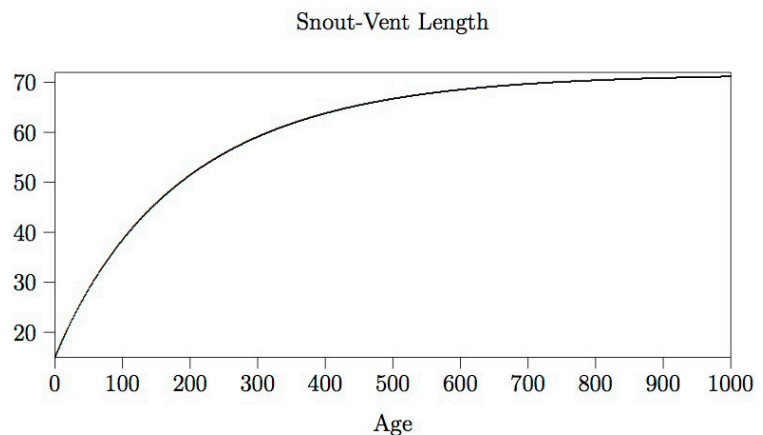
Snout-Vent Length

Figure 1.23: Snout-vent length in mm as a function of age in days assuming 3.5 hrs foraging hours per day, every day.

optimally foraging female as a function of the age at which she stops growth and switches to producing eggs. Further, assuming density dependence consistent with field data showing a maximum abundance of 100 lizards per 100 sq m, the steady state abundance as a function of body size is predicted. According to density-dependent natural selection theory (*K*-selection) the body size that maximizes the steady-state abundance is the optimal body size. The figure above shows the optimal body size for females to be about 45 mm, as in fact observed. This example illustrates a complete and successful modeling protocol that begins with properties of an individual and culminates in an evolutionary prediction of the adult body size for lizards on an island in the absence of congeneric competitors.
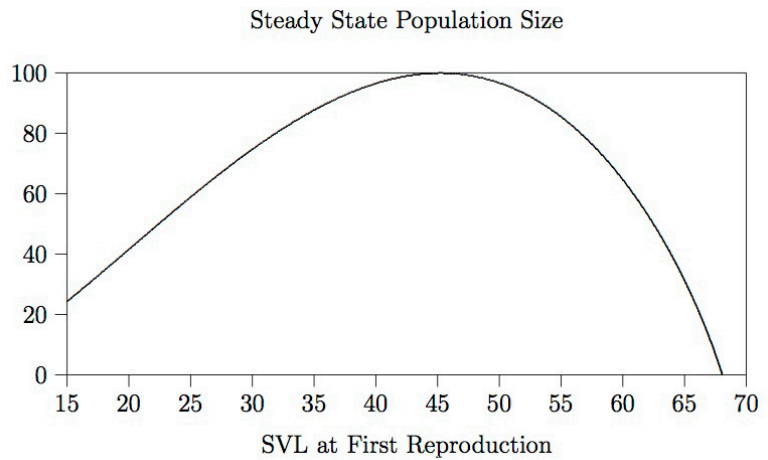
The logic to this model is clearly bottom-up and in the spirit of deriving population-level predictions from the explicit properties of individuals. Nonetheless, this model fails every one of the four Grimm/Railsback criteria. It would be considered as "individually oriented", although not an IBM per se.

(2) Population dynamics of barnacles on an open stretch of rocky intertidal habitat. The figure below offers a schematic diagram of the system of ocean currents off the coast of California and Oregon. Barnacles are small crustaceans whose adult phase lives attached to rocks in the zone between low and high tides. These animals release tiny shrimp-like larvae that live in the surface waters eating phytoplankton until they grow to a size large enough to attach to a rock, whereupon they metamorphose into adults. I developed a model for the population dynamics of these organisms (Roughgarden et al 1988). In the model, one equation pertains to the rate at which larvae settle out from the water onto vacant space on rocks.
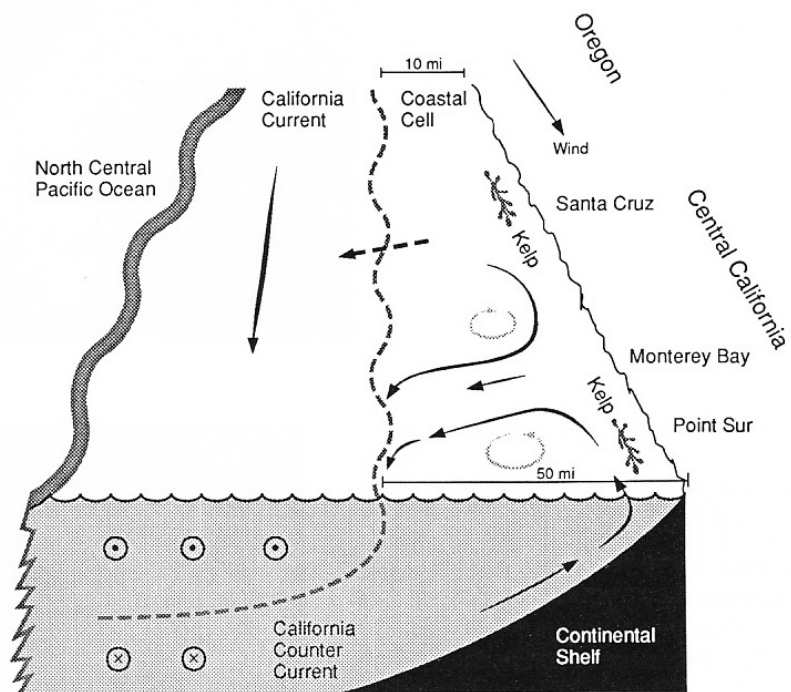
Another equation pertains to the flow of larvae in the offshore currents. These two equations are coupled at the ocean-land boundary. Together they express a model for the population dynamics of barnacles. This model is formulated using a bottom-up logic based on the mechanisms for occupying space and the release of space following mortality. This model might is a "mechanism based model," or MBM, but the state variables are the number of barnacles per area of rock and the number of larvae per surface area of ocean, both of which are real numbers not restricted to integers. This model too fails to satisfy any of the Grimm/Railsback criteria, but could be considered "individually oriented" although not an IBM as such.

These examples show that "individually oriented" models are sufficient to achieve the goal of a "fundamentally new view of ecological systems and processes" as compared with the differential equations of classic population biology dating to the 1940's and earlier. In contrast, IBMs as defined by Grimm and Railsback seem primarily applicable only to very large organisms such as vertebrates and trees, and even then might be worthwhile only for special applications where the individuals are each specifically identified, tagged and tracked.

Individuality Confused with Agency: The difference between an individual based model and an agent based model (ABM) is confusing, with most workers considering these terms to be synonymous. For example, Castiglione (2006) writes, "An entity is an `agent' if it has some degree of autonomy, that is, if it is distinguishable from its environment by some kind of spatial, temporal, or functional attribute. That is, an agent must be identifiable. Moreover, we further require that agents must have some autonomy of action and that they must be able to engage in tasks in an environment without direct external control." Thus, identifiability and autonomy make an entity an agent in the IBM literature. So in this sense, "agent" and "individual" are roughly equivalent. Similarly, Peck (2012) writes "I follow Railsback and Grimm and make no distinction" between IBMs and ABMs. He adds that "grains of sand ... might be considered model agents ... although they do not make choices."

However, I think it is better to use the term "agent" more narrowly--to refer specifically to a goal-seeking individual, where the goal is to increase the individual's fitness, such as the optimally foraging lizard mentioned above. Furthermore, I require that prior to each realized action, an individual has a choice of one or more alternatives and choses the action it carries out according to the criterion that (it thinks) its fitness would thereby increase. So, to most workers an IBM and ABM are synonymous, where as in my definition, an ABM is a subset of IBM in which the individual chooses actions to pursue the goal of increasing its fitness. Choice and fitness-seeking define a biological agent.

Individuality Confused with Programming Metaphor: The definition of an IBM that most workers employ anticipates that the model will be developed using object oriented programming methods. The figure below is drawn from an Apple Computer publication about programming for the iPhone and iPad using the language Objective-C (Apple Inc. 2010). The idea, say for a hand-calculator application, is that a constellation of objects exists, such as the number and function keys together with a viewing screen as well as

some entities called a controller and a model. An event transpires such as someone pressing a key like "7", which triggers a controller to causes a "7" to be displayed on the view. If another "7" is pressed the controller causes another "7" to be displayed, and if a "+" is pressed the controller sends the previous numbers to a model who adds them and sends the result back to the controller for display. The point here is that this
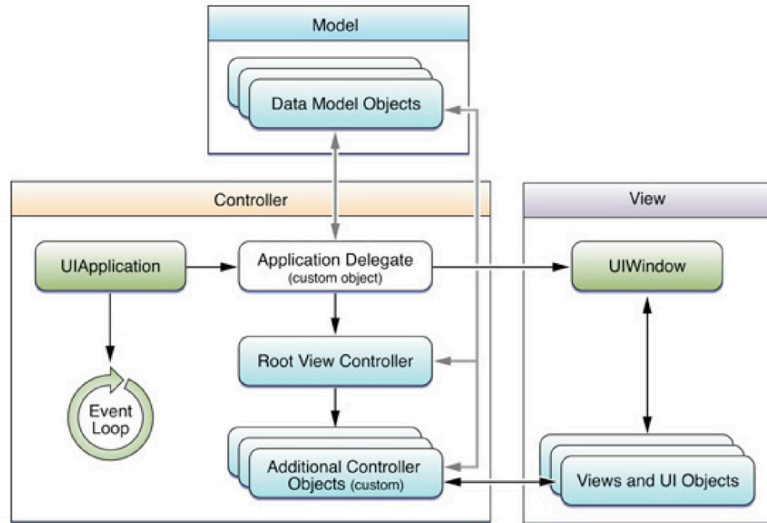
programming metaphor envisions a bunch of interacting agents each with unique capabilities that collectively produce realize a function, such as a hand-calculator application, not immediately evident from inspecting the properties of the individual agents. The notion of a hand-calculator could be said to emerge from the aggregate action of the constituent components. However, what the calculator does in any instance depends on random events. The calculator just sits there endlessly, so to speak, awaiting random keys presses from a user, and then exhibiting results, all without any direction.

The object-oriented programming metaphor differs from the procedural programming metaphor, which is perhaps best envisioned with the analogy of a recipe for cooking. Indeed, the now-classic language, Pascal, is explicitly set up to enforce writing a program like writing a recipe: list the ingredients at the beginning--what the variables are and what operations are allowed on them, and then move to how the ingredients are combined to produce a chocolate cake. Procedural programming envisions a directionality, from input to output, from beginning to end.
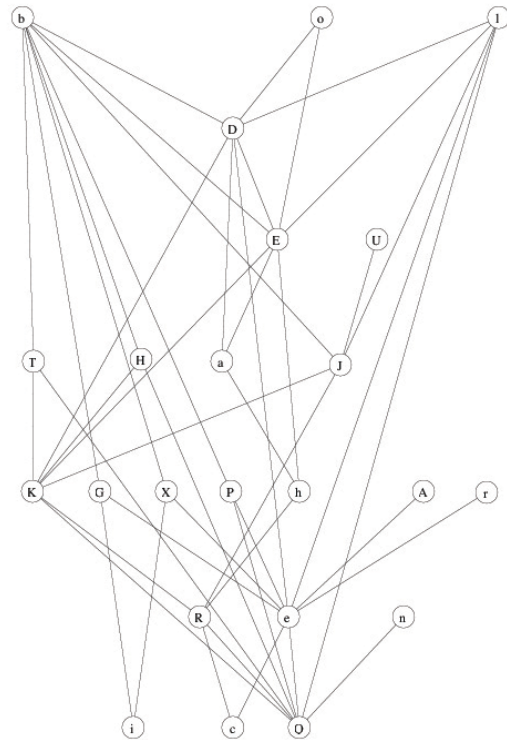
Species coding: A. Adult spider D. *Anolis gingivinus* E. *Anolis pogus* G. Bananaquit H. Bullfinch J. Big floor insects K. Small floor insects P. Elaenia Q. Fruit and seeds R. Fungi T. Grassquit U. Gray Kingbird X. Hummingbirds a. Juvenile spider b. Kestrel c. Leaves e. Canopy insects h. Tiny floor insects i. Nectar and floral l. Pearly-Eyed Thrasher n. Scaly-Breasted Thrasher o. Nematodes r. Yellow Warbler

Both these programming metaphors are useful in ecology, but should not be confused with the issue of whether a model is formulated bottom-up (ie, "individually oriented") vs top down. Indeed, consider the populations comprising a food web. The figure above illustrates a simplified version of a complex food web for the terrestrial community on St. Martin in the Eastern Caribbean (Roughgarden 1995). Like the hand-calculator previously mentioned, a community just sits there. Something happens to one component, like a rain squall that causes the insects on the forest floor to prosper, which in turn causes the spiders and lizards to prosper, which in turn causes the kestrel to prosper, which in turn causes increased deposition to the detritus layer and so on. The community sits there, bubbling away, without any direction--a perfect system for object-oriented programming where the populations in the community are the objects.

In contrast, a biological population is a directional entity. It grows in abundance, and adapts through evolution--a perfect system for procedural programming. It is ironic that object-oriented IBMs have been applied to population dynamics when the natural application of the approach is to communities. In any case, the value of an object-oriented programming vs a procedural programming metaphor should not be confused with the value of a bottom-up individual-oriented protocol vs a top-down protocol for model formulation

Conclusion: IBMs and ABMs originated in the 1960s when mainframe computers were first becoming available to ecological researchers. These computers provoked interest in using computer simulation for ecological modeling rather than relying on mathematical analysis. In judging the merits of model craftsmanship based on simulation vs analysis, I usually come down on the side of analysis. With simulation it may be impossible to drill down to what assumptions are responsible for conclusions, to discern the causal connections between initial conditions and results, and simulation invites unsophisticated and sloppy research together with naive hocus-pocus about the magic of emergence.

Ecological workers with IBMs and ABMs not only bear the burden of avoiding an uncritical embrace computer simulation, they risk shooting themselves in the foot. First, they propose unnecessarily restrictive definitions of what can count as an IBM, definitions that turn out to be inconsistent with usage of IBM workers in different domains. Second, they fail to distinguish between a living organism who acts through choice to increase its fitness and a dead particle. Third they confuse taking an individual organism as the conceptual starting point for ecological theorizing with the choice of programming metaphor--object oriented programming vs procedural programming. Ecological IBM and ABM workers need to clean up their act on these matters least they ruin a good thing.

Specifically, I recommend that the following definitions be adopted: (1) an IBM shall be any model for which the properties of the higher level are derived from properties at the lower level--ie, an IBM is any model formulated with bottom-up logic, any model that is "individual oriented". (2) an ABM shall be any IBM in which the individuals at the lower

level are goal-seeking and take actions based on choices that maximize their goal. (3) Use of object-oriented programming vs procedural programming shall be considered irrelevant to the designation of a model as an IBM or ABM, and shall be undertaken according to what seems most natural to the application.

IBMs and ABMs, as distinct from computer simulation itself, offer three new conceptual advantages. First, they emphasize and implement a bottom up style of formulating ecological models--from a lower level to a higher level, eg., from an individual to social groups and thence to a population, or from organs to an organism. This perspective contrasts with traditional modeling in theoretical ecology based on the logistic and Lotka-Volterra competition and predator-prey equations. It also contrasts with the top-down approach to animal behavior required by Maynard Smith's (1982) population-genetic based solution concept of the evolutionarily-stable strategy (ESS), a approach that begins with the population's gene pool and trickles down to individual behavior.

Second, IBMs and ABMs stress an alternative programming metaphor for ecological systems--the metaphor of object-oriented programming rather than procedural programming. This metaphor seems best for modeling ecological communities where the "objects" are species united through a common food (or interaction) web, and not for modeling populations whose dynamics still seem best represented through a procedural programming metaphor that represents the directionality of population growth and natural selection.

Third, the use of ABMs strongly endorses taking the individual as the fundamental focal or "first class" object for ecology and evolution--working up from the individual to populations and communities or down from the individual to the genes within them. Resting evolutionary theory on ABMs would contrast starkly with population genetics that takes the gene as the fundamental object, and works up from there to the phenotype, the population, and beyond. The agent oriented approach in ecology contradicts the widely shared perspective in evolutionary biology that, as Dawkins (1976) articulated, ``Our genes made us. We animals exist for their preservation and are nothing more than their throwaway survival machines." Instead, according to agent-based ecology, whole individuals are the primary actors on the evolutionary stage, and the genes within them but a stage crew of temporary workers hitchhiking along for the evolutionary ride.

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