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The Virtual Ecologist

By Easton White and Alan Hastings

Isle Royale is perhaps one of nature's best natural experiments. The small island is located in Lake Superior, about 25 kilometers from the Minnesotan mainland. Over 100 years ago, moose began to inhabit the island; wolves followed in the late 1940s. Wolves are the only predators of the moose and hunt them almost exclusively. This dynamic established an idealized predator-prey system that researchers have studied for the last six decades.

Suppose we want to better understand the role of climate in this predator-prey system. To do so, a biologist would first create hundreds of exact replica Isle Royales, each with different climatic conditions over several decades of experiment (due to the long generation times of the relevant species). This would allow us to examine past climatic effects as well as future impact on the predator-prey relationship. Of course, such an experiment would be ridiculous and impossible. This is what makes ecology difficult. Data is sparse, experiments can be challenging (if not unfeasible), and our actions affect the systems under study. We can, however, perform these experiments in silico; in other words, on our computers.

Moose began inhabiting Lake Superior's Isle Royale as early as the 1900s; now they are an iconic part of the ecosystem. Image courtesy of the National Park Service.

Mathematical models have a long history in the field of ecology. Italian mathematician Leonardo of Pisa (commonly known as Fibonacci) developed perhaps the earliest model of population growth around the year 1200. He envisioned a scenario where a pair of newborn rabbits were allowed to grow and reproduce. Assuming rabbits can reproduce at one month of age, one rabbit pair would exist at the end of the first month, two rabbit pairs at the end of the second month, three rabbit pairs after the third month, and so forth. This leads to the Fibonacci sequence.

Ecology has come a long way since Fibonacci's time. In 1838, Pierre-François Verhulst applied the logistic function to model populations whose growth depended on population size. In the early 1900s, Alfred Lotka and Vito Volterra independently developed differential equations to study both competition and predator-prey dynamics. The advancements continue to this day. Researchers have gained a better understanding of simple population models and built more detailed and specific models. These improvements occur because of new questions and novel tools, including increased computational power. Several authors have examined the role of models in ecology. Richard Levins emphasized the trichotomy between generality, realism, and precision in models [6]. Evelyn Pielou categorized models into different types—including models for forecasting and models for understanding—based on their applications [10]. We build on these papers with a discussion and examples of the main uses of models in practice today.

Seeking Understanding

Perhaps the most common purpose of a model is to better understand how the natural world works. One can do so by reducing nature to extremely simple models—like the Lotka-Volterra differential equations to represent competition—or building more detailed models that are comparable with real systems.

Brett Melbourne and Alan Hastings utilized a series of stochastic, discrete-time models to better understand the growth and spread of *Tribolium spp.*—an invasive pest better known as the flour beetle—in a laboratory setting [9]. These models varied in complexity, ranging from those with only demographic stochasticity to those with environmental stochasticity and biases in the sex ratio. Melbourne and Hastings compared their models to actual experimental data and determined that the most complicated, detailed models were required to explain spatial spread.

Elisa Benincà and her collaborators also built models to study nature, examining a rocky intertidal community that cycled between bare rock, barnacles and algae, and mussels [1]. The team sought to determine the drivers of this cyclic behavior, but only had a single replicate. Therefore, they built a model of differential equations and included temperature as a seasonal forcing term. Benincà et al. discovered that sustaining the cyclic oscillation required seasonal changes in temperature. This discovery would have been impossible without a detailed model where one could vary seasonal changes — an impractical field experiment.

Making Predictions

One of the most desired benefits of models is undoubtedly their ability to make predictions about the natural world. For instance, one might wish to forecast the number of fish that will populate a fishery in the coming year. In the age of big data, researchers can combine streams of data to predict future fish populations. Yet this process only works with a lot of available data and—most importantly—a similarity between the future and the past. As another example, scientists have used models to calculate future species distributions under the influence of climate change. Such models rely on past occurrence data—correlated with environmental conditions—to extrapolate into the future. They do not often include details on dispersal limitations or species interactions. In a changing world, process-based (or mechanistic) models are necessary for prediction. These models can be difficult to build because they require an understanding of the system's underlying processes. However, they integrate uncertainty and provide transparent assumptions, making them appropriate for projection [3].

Wolves have been the primary predator of moose on Isle Royale, a small island in Lake Superior, since 1948. Image courtesy of the National Park Service.

Generating Hypotheses

One of the most fruitful uses of mathematical models has been in the development of new hypotheses about the natural world. Early work by Lotka and Volterra gave rise to the predator-prey equations that bear their names. They found that predators and prey could coexist with cyclic behavior. In 1934, Georgii Gause tested these hypotheses in protozoan predator-prey experiments [4]. He found that typically, predators quickly drive prey to extinction — which was not in line with Lotka and Volterra's predictions. Gause instead discovered conditions (e.g., prey refuges) that enabled coexistence. Decades later, Robert May suggested that complex dynamics (e.g., limit cycles, chaos) could arise from simple discrete-time equations [7-8]. This finding resulted in new experiments and field studies to better understand the incidence of these dynamics in nature [5].

Designing Experiments

Mathematical models can also guide experimental design. In a recent paper, Easton White asked how many years lent confidence to estimation of long-term population trends [11]. To address this question in the context of the moose population on Isle Royale, one would need to construct hundreds of new Isle Royales, place a moose population on each, and sample for different lengths of time. This, of course, is not practical. Creating a mathematical model to build virtual moose populations and estimate the minimum time required for confidence is a better alternative [12]. Researchers have utilized this approach to address a variety of other questions and either aid or substitute for experiments. On a related note, because a model formalizes one's thinking about a system, it can also reveal gaps in his/her understanding of that system, which then provide guidance on the types of data one should collect.

Conclusions and Future Direction

Mathematical models have a long history in ecology and will continue to play a large role in the field. This is especially true of more sophisticted models that have resulted from recent advances in computing. As collected field data becomes sufficient for classification as “big data,” models will also become increasingly important in building theory. Additionally, ecological models must also account for rare, black swan-types of events, and come to grips with uncertainty with regard to either parameter estimation or the model structure itself. Approaches like partially observable Markov decision processes have gained traction in dealing with uncertainty [2]. How complicated models should become remains an open question.

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