must consider the basic underlying models of evolutionary genetics. Thus, there are good treatments of how to conceptualize fitness, model allele frequency change, and derive equilibria and examine their stability. McElreath and Boyd clearly see George Price's covariance approach to evolution and selection as fundamental. They use it not only in the context in which it is most often discussed, the derivation of Hamilton's rule, but also in numerous other places. Indeed, the most impressive thing to be taken from the book is how, at a sufficiently abstract level, the principles underlying areas as apparently diverse as kin selection, cooperation, signaling, and sex allocation are largely the same.

The authors deliberately intersperse the introduction of the general mathematical heavy machinery with case studies on topics that are of interest to students of evolution and human behavior. The topics covered include conflict resolution, kin selection, reciprocity and collective action, signaling, the evolution of social learning, levels of selection, sex allocation, and sexual selection. Along the way, the more frequent misunderstandings of evolutionary ideas are very patiently exposed. For example, there is a nice treatment of why the coefficient of relatedness is not the probability of two individuals sharing the same allele at a locus. After all, many human alleles are at fixation, and this does not mean we all have r=1. Similarly, we are shown how Hamilton's rule relies on selection not being too strong and thus avoids the problem of the kin-directed self-sacrifice mutant allele instantly driving itself extinct.

All in all, this is a fantastically stimulating and useful book for anyone who wants to think about a topic of study from a Darwinian point of view. Understanding the principles within it can help move a graduate student or researcher from being someone who waits patiently at the outlet of the evolutionary theory black box to someone who is comfortable playing around with the machinery itself. The book is about as accessible as it is possible for it to be, but it is, of course, very mathematical. The chapter on sexual selection in particular is quite hard going. However, there is surprisingly little that is too challenging for anyone comfortable with basic algebra and calculus. The style is—if this makes sense for a book of mathematics—quite informal, going directly for the main conceptual principles. Problems and work solutions are also provided.

If we are to produce a fruitful iterative cross-talk between theory and data in the study of evolution and human behavior, then we should all try to get on top of the principles elaborated here. Whether everyone will is another matter. Stephen Hawking commented in his book, *A Brief History of Time*, that every equation in a book halves its potential readership. If true, this would leave *Mathematical Models of Social Evolution: A Guide for the Perplexed* largely unread. However, the payoff for the field is too great for this to happen, and I hope this book becomes a standard reading for graduate students of evolution and human behavior.

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Are readers of *Evolution and Human Behavior* interesting people? A review of Hanna Kokko's *Modelling for Field Biologists and Other Interesting People.*

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> "Any sufficiently advanced technology is indistinguishable from magic." Arthur C. Clarke's third law

Utter the word "model" in certain academic circles and you are sure to generate controversy. Some complain that, while useful, the mathematics are beyond them. Others, with or without confidence in their math abilities, assert that models do not tell you anything you did not know or could not have already known. Still others believe models to be useful, but it is, alas, too late for them to begin the training in these arcane skills.

As few researchers are trained in a diversity of modeling techniques, building models often seems magical. Nothing could be further from the truth. Just like well-designed experiments, carefully constructed models seek to reveal the causal relationships between variables, all else being equal. While experiments seek to know if something occurs in nature, models serve as existence proofs, putting verbal logic to a more precise test. We believe that it is crucial for evolutionary behavioral scientists to add this kind of modeling to their methodological skills set. Even if one's goal is not to make models, one should still be an educated consumer of them.

Unfortunately, learning to decipher and develop models can be difficult. The problem is finding the right guide. In addition to publishing important theoretical contributions, such as unifying Fisher's runaway hypothesis and Zahavi's good genes model (Kokko, Brooks, McNamara, & Houston, 2002), Kokko has written an excellent accessible introductory text on ecological and evolutionary modeling. As the title suggests, this book is intended for those with "no hands-on experience with mathematical modelling so far" (p. ix).

1. A model of the book

Kokko's philosophy is to build models as simply as possible. She rightfully concedes that reality is a tangle of causes and effects where everything interacts with everything else. Right away, she discourages us from building "complex" models. Even if we could, why should we? Kokko asks us to imagine a cartographer making a map that is on the same scale as the geography being catalogued. Such a model is worse than useless, as if you have substituted one complexity you do not understand for another. Like a good map, a model should be built for a specific purpose, stripping away unnecessary detail and providing a clear picture of what is important.

Each chapter begins with a brief overview of an interesting biological phenomenon, such as partial migration, and then distills a key question, such as: Why are there species of birds in which some individuals migrate, while others do not? Having defined the problem, Kokko guides us through the process of building a model: Choose a minimal set of explicit assumptions, decide how variables interact, and then follow the logic to its conclusion. While she provides some analytic derivations, what makes this book unique is that Kokko goes into great detail presenting numerical solutions plus the programming code necessary to replicate and further explore these models. For those who are not adept at the mathematics, this is an excellent primer to building ecological and evolutionary models. Each chapter presents an encapsulated introduction of a different modeling technique and, for those who want to delve deeper, concludes with an up-to-date guide to that particular literature.

2. Genetics models

Kokko covers genetics models in two chapters. The first modeling technique we meet is *population genetics*, which tracks the effect of evolutionary forces on changes in allele frequencies. Considering sexual conflict, Kokko poses the question: Can a heritable trait spread if it aids male reproduction at the expense of female fitness?

Population genetics models become tedious, however, when dealing with multiple loci and multiple alleles. For this, we turn to *quantitative genetics*. As many traits of interest, such as height, are the products of many loci and thus vary continuously, one can represent populations as distributions, keeping track of statistics such as means and variances. This chapter considers a situation in which a cue to predation risk varies and developing organisms must "decide" between a defended or an undefended adult phenotype. Here, Kokko reviews the concept of a reaction norm (i.e., a life-history response to an environmentally determined cue, often called *evoked culture* in evolutionary psychology; Tooby & Cosmides, 1992) that defines a threshold cue value that pushes development from one morph to the other.

3. Phenotypic models

The majority of the book explores phenotypic modeling techniques. By assuming that the underlying genetics imposes no constraints on natural selection, we can safely ignore the evolutionary dynamics and focus on adaptations. This phenotypic gambit assumes sufficient evolutionary time to generate optimal phenotypes. If this sounds familiar, it should; cognitive scientists often assume that the underlying neural structure imposes no constraints on cognition. While a lot of ink has been spilled on differentiating human behavioral ecology and evolutionary psychology, both fields employ similar gambits. The former assumes that behavior is optimal in current environments, while the latter assumes that selection has optimized behavior over ancestral environments.

In a chapter on *optimization methods*, Kokko explores the conditions under which signals can be honest. Fitting our intuitions, a preliminary model shows us that when costs decrease nonlinearly with increasing quality, higher-quality males signal more vigorously. However, such results crucially depend on the assumptions. In a subsequent model, when the relationship between survival and quality is S-shaped, honest signals (i.e., higher-quality males signal more) only evolve when the overall condition of the population is quite low. When the population as a whole is in better condition, higher-quality males signal less, instead choosing to invest resources in growth and development.

When decisions trade off intertemporally (e.g., today's decisions affect tomorrow's options), it is no longer sufficient to optimize each decision in isolation. In *dynamic optimization*, we find the policy, which defines what an organism ought to do for every decision in every possible state, that maximizes total fitness. Counterintuitively, finding such an optimal policy begins by starting at the end and then recursively working back to the beginning. To illustrate, Kokko models the foraging behavior of a bird, whose goal is to survive a cold winter's day. In each time period, the bird must trade off between building up fat reserves and minimizing predation risk.

When the fitness of an organism is dependent not only on its own behavior but also on the behavior of other organisms, different modeling techniques are required. In a chapter on *game theory*, Kokko asks how tall should a tree be, assuming other trees want their day in the sun, too. Building on this, she covers *evolutionary invasion analysis*, which takes into account that fitness depends not only on what others do but also on how many others are present.

4. Agent-based simulations

As a model can become analytically intractable, Kokko devotes a full chapter to *individual-based simulations*. Here, the rules by which individual organisms behave are specified and the consequences of those rules are tracked over time. Other advantages of simulations include providing checks to analytic results and brainstorming in the early stages of modeling. However, while researchers often justify simulations by stressing the importance of adding realism through randomness, Kokko reminds us that this is not true; analytic models can handle stochasticity. Furthermore, as computing power becomes faster and cheaper, it is tempting to keep adding parameters to gain more realism. As the number of parameters increases, it becomes increasingly unlikely that the whole parameter space can be explored. As a result, simulations are often limited in showing that something can happen, but not that something cannot happen.

5. A bridge to somewhere

We believe that readers of this journal will profit from reading this book. Even for those already familiar with a specific modeling technique, being adept in a multitude of techniques allows the researcher to ask different, but related questions and to find converging lines of evidence. As the psychologist Abraham Maslow remarked, when the only tool you have is a hammer, every problem begins to resemble a nail.

For instance, although students of human behavioral ecology are familiar with optimization methods, many of their questions might benefit from dynamic optimization techniques. The transition from hunter gathering to agriculture involves intertemporal tradeoffs. Even though agriculture might yield higher overall returns, would-be farmers must consume enough food each day of the year, even though they harvest only once a year (or twice, if you live in California like we do). Similarly, dynamic optimization might shed light on life-history phenomena ranging from menarche to marriage to menopause.

While research areas such as cooperation and reciprocity suffer from too much modeling, with little emphasis on empirical verification, it seems to us that evolutionary psychology often suffers from the opposite problem. The common procedure is to posit a recurrent adaptive problem faced by our ancestors; verbally deduce an adaptation that solves the problem; generate predictions about what types of behaviors, attitudes, and so on, such adaptations would manifest; and, finally, test those predictions with humans. In principle, nothing prevents this kind of research from being translated into formal models, thereby putting verbal logic to a more rigorous test, making theories more transparent, and allowing related arguments to be more easily compared. Consider, for example, the study of menstrual cycle effects to make inferences about evolved mating strategies. While these studies generate interesting results, building models would force the researcher to more explicitly lay out assumptions and demonstrate that, from those assumptions, natural selection would result in the proposed adaptations. Our discipline should seamlessly integrate modeling and empirical research.

6. We use MATLAB. Why don't you, too?

In keeping with the theme of expanding skills sets, Kokko illustrates all of the modeling techniques using MATLAB (MathWorks, Inc., Natick, MA). MATLAB is an easy-to-learn, yet extremely powerful computing language and interactive environment for, say, data visualization and statistical analysis, designing graphical user interfaces, numerical computation, individual-based simulations, and symbolic mathematics. Using a domain-general platform such as MATLAB saves you from using separate software for each of your routine scientific tasks (e.g., doing statistics, creating publication-ready plots, and conducting experiments). To boot, MATLAB is supported on all platforms (PC, Mac, and Linux) and is relatively inexpensive, especially if you are a student. While Kokko provides a "quick and informal guide to MATLAB" (p. 194), more thorough introductions are available (e.g., Rosenbaum, 2007).

7. Conclusion

So, whether you are the scarecrow who thinks of yourself as not having the right kind of mind, the courage-challenged lion who does not think of yourself as capable of learning a new skills set, or the tin man who does not think of yourself as having a passion for modeling, we think this book will prove otherwise. In our rendition of *Wizard of Oz*, Kokko becomes Dorothy, taking the reader on a journey through the wonderful world of modeling, putting to rest any fears, distrusts, or misgivings. Rest assured, the analogy between a model and a great story runs deeper than our whimsy. While Kokko's book can be read straight through, modeling, like writing fiction, involves practice. By straying from the path, taking the time to question her assumptions, testing her computer code, and seeing the results for oneself, a richer understanding results. With this book, Kokko, our faithful guide, pulls back the curtain, replacing suspicions of magic with a deep appreciation for how models, such as art, do not seek to recreate, but rather to reveal, the inner workings of their subject matter.

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