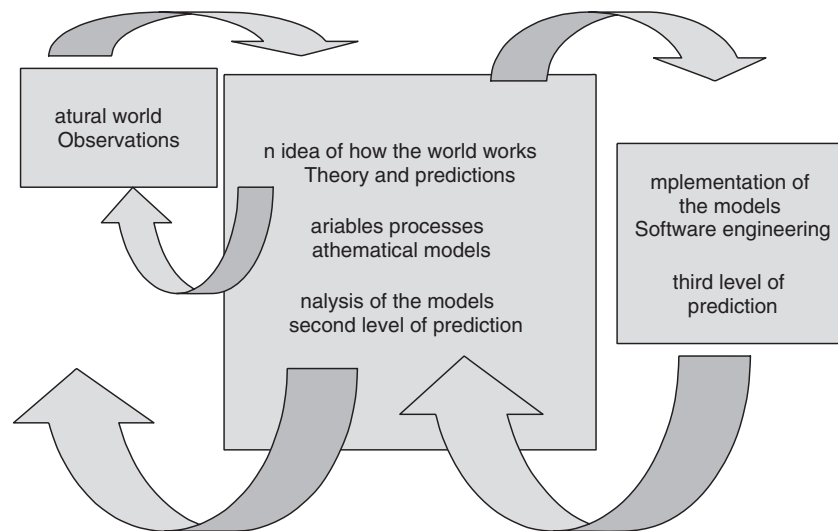


Chapter 1

Four examples and a metaphor

Robert Peters (Peters 1991) – who (like Robert MacArthur) tragically died much too young – told us that theory is going beyond the data. I thoroughly subscribe to this definition, and it shades my perspective on theoretical biology (Figure 1.1). That is, theoretical biology begins with the natural world, which we want to understand. By thinking about observations of the world, we conceive an idea about how it works. This is theory, and may already lead to predictions, which can then flow back into our observations of the world. Theory can be formalized using mathematical models that describe appropriate variables and processes. The analysis of such models then provides another level of predictions which we take back to the world (from which new observations may flow). In some cases, analysis may be insufficient and we implement the models using computers through programming (software engineering). These programs may then provide another level of prediction, which can flow back to the models or to the natural world. Thus, in biology there can be many kinds of theory. Indeed, without a doubt the greatest theoretician of biology was Charles Darwin, who went beyond the data by amassing an enormous amount of information on artificial selection and then using it to make inferences about natural selection. (Second place could be disputed, but I vote for Francis Crick.) Does one have to be a great naturalist to be a theoretical biologist? No, but the more you know about nature – broadly defined (my friend Tim Moerland at Florida State University talks with his students about the ecology of the cell (Moerland 1995)) – the better off you'll be. (There are some people who will say that the converse is true, and I expect that they won't like this book.) The same is true, of course, for being able to

Figure 1.1. Theoretical biology begins with the natural world, which we want to understand. By thinking about observations of the world, we begin to conceive an idea about how it works. This is theory, and may already lead to predictions, which can then flow back into our observations of the world. The idea about how the world works can also be formalized using mathematical models that describe appropriate variables and processes. The analysis of such models then provides another level of predictions which we can take back to the world (from which new observations may flow). In some cases, analysis may be insufficient and we choose to implement our models using computers through programming (software engineering). These programs then provide another level of prediction, which can also flow back to the models or to the natural world.



develop models and implementing them on the computer (although, I will tell you flat out right now that I am not a very good programmer – just sufficient to get the job done). This book is about the middle of those three boxes in Figure 1.1 and the objective here is to get you to be good at converting an idea to a model and analyzing the model (we will discuss below what it means to be good at this, in the same way as what it means to be good at opera).

On January 15, 2003, just as I started to write this book, I attended a celebration in honor of the 80th birthday of Professor Joseph B. Keller. Keller is one of the premier applied mathematicians of the twentieth century. I first met him in the early 1970s, when I was a graduate student. At that time, among other things, he was working on mathematics applied to sports (see, for example, Keller (1974)). Joe is fond of saying that when mathematics interacts with science, the interaction is fruitful if mathematics gives something to science and the science gives something to mathematics in return. In the case of sports, he said that what mathematics gained was the concept of the warm-up. As with athletics, before embarking on sustained and difficult mathematical exercise, it is wise to warm-up with easier things. Most of this chapter is warm-up. We shall consider four examples, arising in behavioral and evolutionary ecology, that use algebra, plane geometry, calculus, and a tiny bit of advanced calculus. After that, we will turn to two metaphors about this material, and how it can be learned and used.

Foraging in patchy environments

Some classic results in behavioral ecology (Stephens and Krebs 1986, Mangel and Clark 1988, Clark and Mangel 2000) are obtained in the

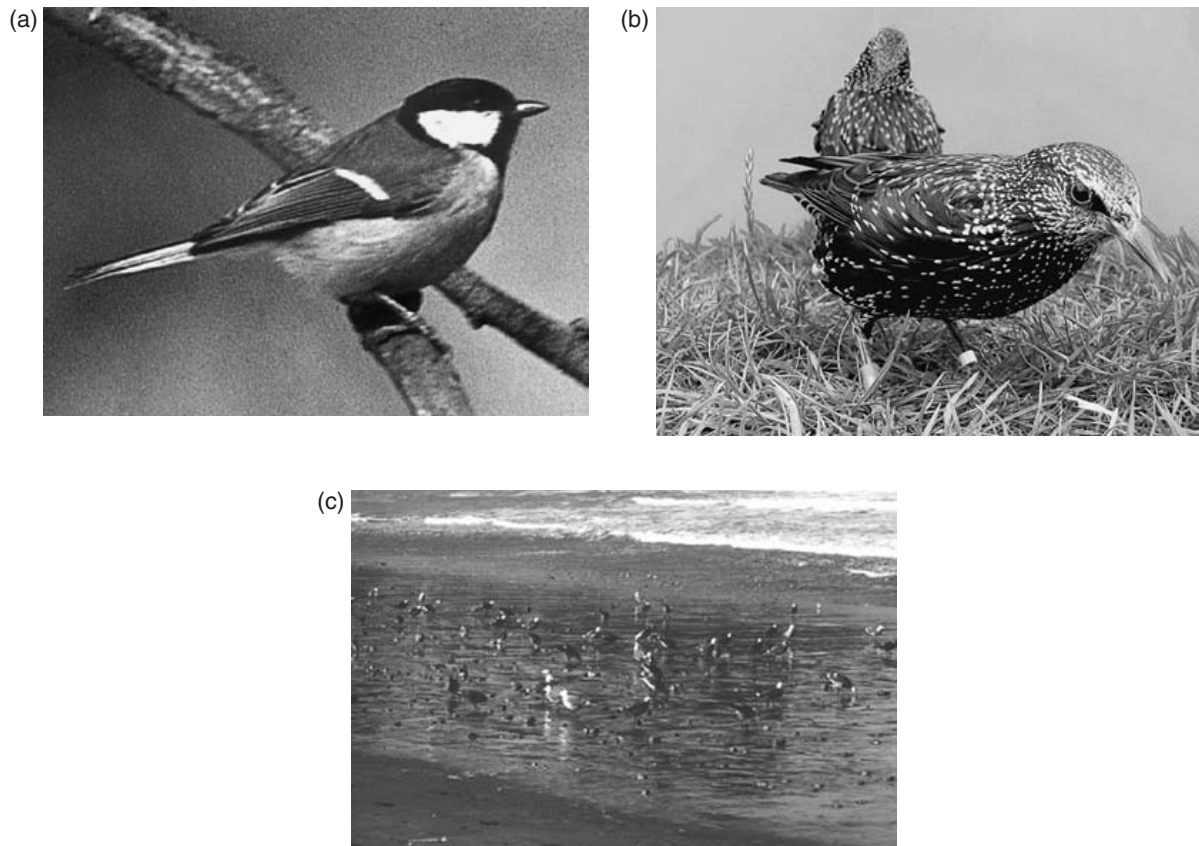


Figure 1.2. Two stars of foraging experiments are (a) the great tit, *Parus major*, and (b) the common starling *Sturnus vulgaris* (compliments of Alex Kacelnik, University of Oxford). (c) Foraging seabirds on New Brighton Beach, California, face diet choice and patch leaving problems.

study of organisms foraging for food in a patchy environment (Figure 1.2). In one extreme, the food might be distributed as individual items (e.g. worms or nuts) spread over the foraging habitat. In another, the food might be concentrated in patches, with no food between the patches. We begin with the former case.

The two prey diet choice problem (algebra)

We begin by assuming that there are only two kinds of prey items (as you will see, the ideas are easily generalized), which are indexed by $i = 1, 2$. These prey are characterized by the net energy gain E_i from consuming a single prey item of type i , the time h_i that it takes to handle (capture and consume) a single prey item of type i , and the rate λ_i at which prey items of type i are encountered. The profitability of a single prey item is E_i/h_i since it measures the rate at which energy is accumulated when a single prey item is consumed; we will assume that prey

type 1 is more profitable than prey type 2. Consider a long period of time T in which the only thing that the forager does is look for prey items. We ask: what is the best way to consume prey? Since I know the answer that is coming, we will consider only two cases (but you might want to think about alternatives as you read along). Either the forager eats whatever it encounters (is said to generalize) or it only eats prey type 1, rejecting prey type 2 whenever this type is encountered (is said to specialize). Since the flow of energy to organisms is a fundamental biological consideration, we will assume that the overall rate of energy acquisition is a proxy for Darwinian fitness (i.e. a proxy for the long term number of descendants).

In such a case, the total time period can be divided into time spent searching, S , and time spent handling prey, H . We begin by calculating the rate of energy acquisition when the forager specializes. In search time S , the number of prey items encountered will be $\lambda_1 S$ and the time required to handle these prey items is $H = h_1(\lambda_1 S)$. According to our assumption, the only things that the forager does is search and handle prey items, so that $T = S + H$ or

$$T = S + h_1 \lambda_1 S = S(1 + \lambda_1 h_1) \quad (1.1)$$

We now solve this equation for the time spent searching, as a fraction of the total time available and obtain

$$S = \frac{T}{1 + \lambda_1 h_1} \quad (1.2)$$

Since the number of prey items encountered is $\lambda_1 S$ and each item provides net energy E_1 , the total energy from specializing is $E_1 \lambda_1 S$, and the rate of acquisition of energy will be the total accumulated energy divided by T . Thus, the rate of gain of energy from specializing is

$$R_s = \frac{E_1 \lambda_1}{1 + h_1 \lambda_1} \quad (1.3)$$

An aside: the importance of exercises

Consistent with the notion of mathematics in sport, you are developing a set of skills by reading this book. The only way to get better at skills is by practice. Throughout the book, I give exercises – these are basically steps of analysis that I leave for you to do, rather than doing them here. You should do them. As you will see when reading this book, there is hardly ever a case in which I write “it can be shown” – the point of this material is to learn how to show it. So, take the exercises as they come – in general they should require no more than a few sheets of paper – and really make an effort to do them. To give you an idea of the difficulty of

exercises, I parenthetically indicate whether they are easy (E), of medium difficulty (M), or hard (H).

Exercise 1.1 (E)

Repeat the process that we followed above, for the case in which the forager generalizes and thus eats either prey item upon encounter. Show that the rate of flow of energy when generalizing is

$$R_g = \frac{E_1\lambda_1 + E_2\lambda_2}{1 + h_1\lambda_1 + h_2\lambda_2} \quad (1.4)$$

We are now in a position to predict the best option: the forager is predicted to specialize when the flow of energy from specializing is greater than the flow of energy from generalizing. This will occur when $R_s > R_g$.

Exercise 1.2 (E)

Show that $R_s > R_g$ implies that

$$\lambda_1 > \frac{E_2}{E_1h_2 - E_2h_1} \quad (1.5)$$

Equation (1.5) defines a “switching value” for the encounter rate with the more profitable prey item, since as λ_1 increases from below to above this value, the behavior switches from generalizing to specializing. Equation (1.5) has two important implications. First, we predict that the foraging behavior is “knife-edge” – that there will be no partial preferences. (To some extent, this is a result of the assumptions. So if you are uncomfortable with this conclusion, repeat the analysis thus far in which the forager chooses prey type 2 a certain fraction of the time, p , upon encounter and compute the rate R_p associated with this assumption.) Second, the behavior is determined solely by the encounter rate with the more profitable prey item since the encounter rate with the less profitable prey item does not appear in the expression for the switching value.

Neither of these could have been predicted a priori.

Over the years, there have been many tests of this model, and much disagreement about what these tests mean (more on that below). My opinion is that the model is an excellent starting point, given the simple assumptions (more on these below, too).

The marginal value theorem (plane geometry)

We now turn to the second foraging model, in which the world is assumed to consist of a large number of identical and exhaustible patches containing only one kind of food with the same travel time between them

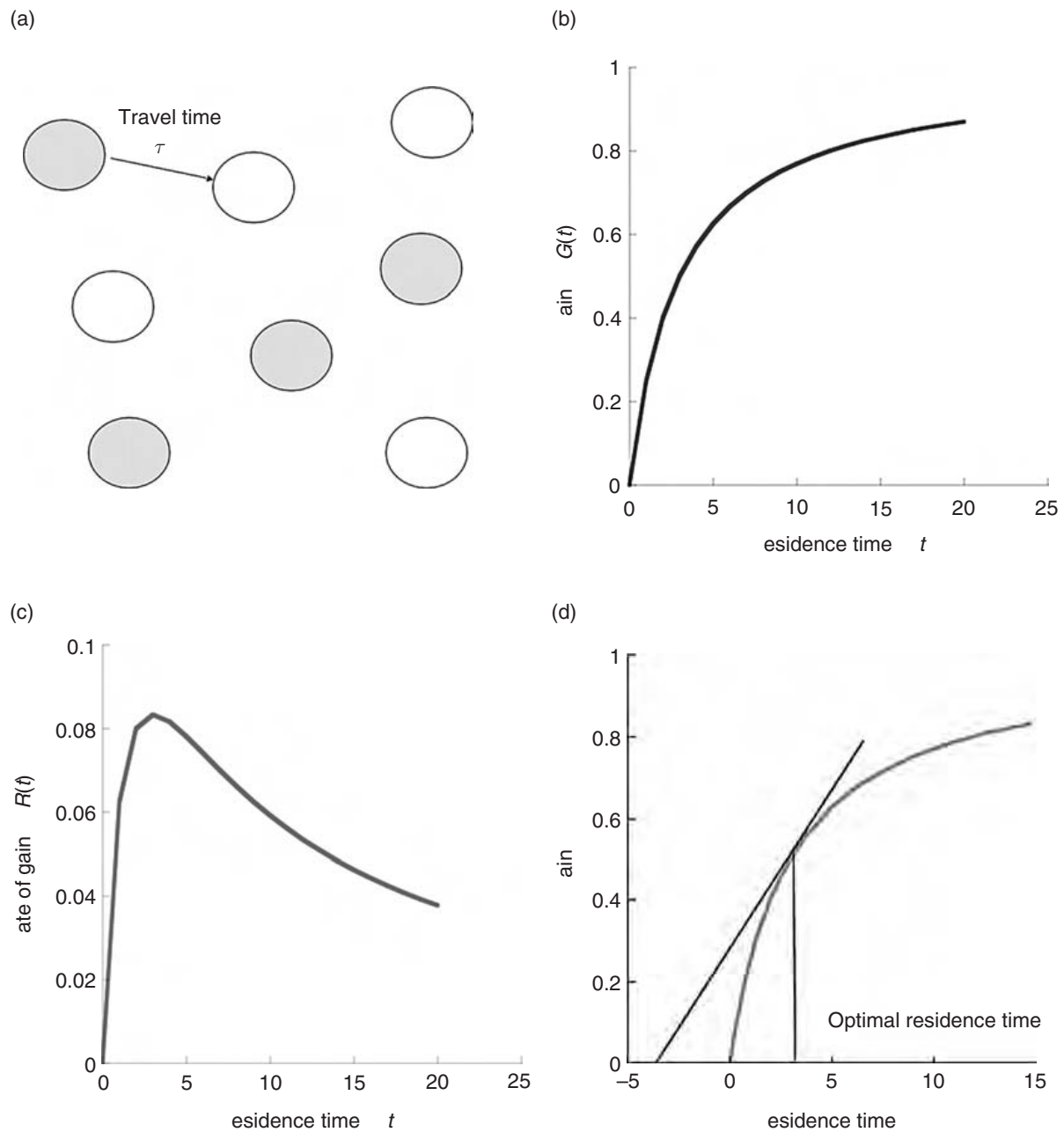


Figure 1.3. (a) A schematic of the situation for which the marginal value theorem applies. Patches of food (represented here in metaphor by filled or empty patches) are exhaustible (but there is a very large number of them) and separated by travel time τ . (b) An example of a gain curve (here I used the function $G(t) = t/(t+3)$), and (c) the resulting rate of gain of energy from this gain curve when the travel time $\tau = 3$. (d) The marginal value construction using a tangent line.

(Figure 1.3a). The question is different: the choice that the forager faces is how long to stay in the patch. We will call this the patch residence time, and denote it by t . The energetic value of food removed by the forager when the residence time is t is denoted by $G(t)$. Clearly $G(0) = 0$ (since nothing can be gained when no time is spent in the patch). Since the patch is exhaustible, $G(t)$ must plateau as t increases. Time for a pause.

Exercise 1.3 (E)

One of the biggest difficulties in this kind of work is getting intuition about functional forms of equations for use in models and learning how to pick them appropriately. Colin Clark and I talk about this a bit in our book (Clark and Mangel 2000). Two possible forms for the gain function are $G(t) = at/(b + t)$ and $G(t) = at^2/(b + t^2)$. Take some time before reading on and either sketch these functions or pick values for a and b and graph them. Think about what the differences in the shapes mean. Also note that I used the same constants (a and b) in the expressions, but they clearly must have different meanings. Think about this and remember that we will be measuring gain in energy units (e.g. kilocalories) and time in some natural unit (e.g. minutes). What does this imply for the units of a and b , in each expression?

Back to work. Suppose that the travel time between the patches is τ . The problem that the forager faces is the choice of residence in the patch – how long to stay (alternatively, should I stay or should I go now?). To predict the patch residence time, we proceed as follows.

Envision a foraging cycle that consists of arrival at a patch, residence (and foraging) for time t and then travel to the next patch, after which the process begins again. The total time associated with one feeding cycle is thus $t + \tau$ and the gain from that cycle is $G(t)$, so that the rate of gain is $R(t) = G(t)/(t + \tau)$. In Figure 1.3, I also show an example of a gain function (panel b) and the rate of gain function (panel c). Because the gain function reaches a plateau, the rate of gain has a peak. For residence times to the left of the peak, the forager is leaving too soon and for residence times to the right of the peak the forager is remaining too long to optimize the rate of gain of energy.

The question is then: how do we find the location of the peak, given the gain function and a travel time? One could, of course, recognize that $R(t)$ is a function of time, depending upon the constant τ and use calculus to find the residence time that maximizes $R(t)$, but I promised plane geometry in this warm-up. We now proceed to repeat a remarkable construction done by Eric Charnov (Charnov 1976). We begin by recognizing that $R(t)$ can be written as

$$R(t) = \frac{G(t)}{t + \tau} = \frac{G(t) - 0}{t - (-\tau)} \quad (1.6)$$

and that the right hand side can be interpreted as the slope of the line that joins the point $(t, G(t))$ on the gain curve with the point $(-\tau, 0)$ on the abscissa (x -axis). In general (Figure 1.3d), the line between $(-\tau, 0)$ and the curve will intersect the curve twice, but as the slope of the line increases the points of intersection come closer together, until they meld when the line is tangent to the curve. From this point of tangency, we can read down the optimal residence time. Charnov called this the marginal value theorem, because of analogies in economics. It allows us to predict residence times in a wide variety of situations (see the [Connections](#) at the end of this chapter for more details).

Egg size in Atlantic salmon and parent–offspring conflict (calculus)

We now come to an example of great generality – predicting the size of propagules of reproducing individuals – done in the context of a specific system, the Atlantic salmon *Salmo salar* L. (Einum and Fleming 2000). As with most but not all fish, female Atlantic salmon lay eggs and the resources they deposit in an egg will support the offspring in the initial period after hatching, as it develops the skills needed for feeding itself (Figure 1.4). In general, larger eggs will improve the chances of offspring survival, but at a somewhat decreasing effect. We will let x denote the mass of a single egg and $S(x)$ the survival of an offspring through the critical period of time (Einum and Fleming used both 28 and 107 days with similar results) when egg mass is x . Einum and Fleming chose to model $S(x)$ by

$$S(x) = 1 - \left(\frac{x_{\min}}{x}\right)^a \quad (1.7)$$

where $x_{\min} = 0.0676$ g and $a = 1.5066$ are parameters fit to the data. We will define $c = (x_{\min})^a$ so that $S(x) = 1 - cx^{-a}$, understanding that $S(x) = 0$ for values of x less than the minimum size. This function is shown in Figure 1.5a; it is an increasing function of egg mass, but has a decreasing slope. Even so, from the offspring perspective, larger eggs are better.

However, the perspective of the mother is different because she has a finite amount of gonads to convert into eggs (in the experiments of Einum and Fleming, the average female gonadal mass was 450 g). Given gonadal mass g , a mother who produces eggs of mass x will make g/x eggs, so that her reproductive success (defined as the expected number of eggs surviving the critical period) will be

$$R(g, x) = \frac{g}{x} S(x) = \frac{g}{x} (1 - cx^{-a}) \quad (1.8)$$

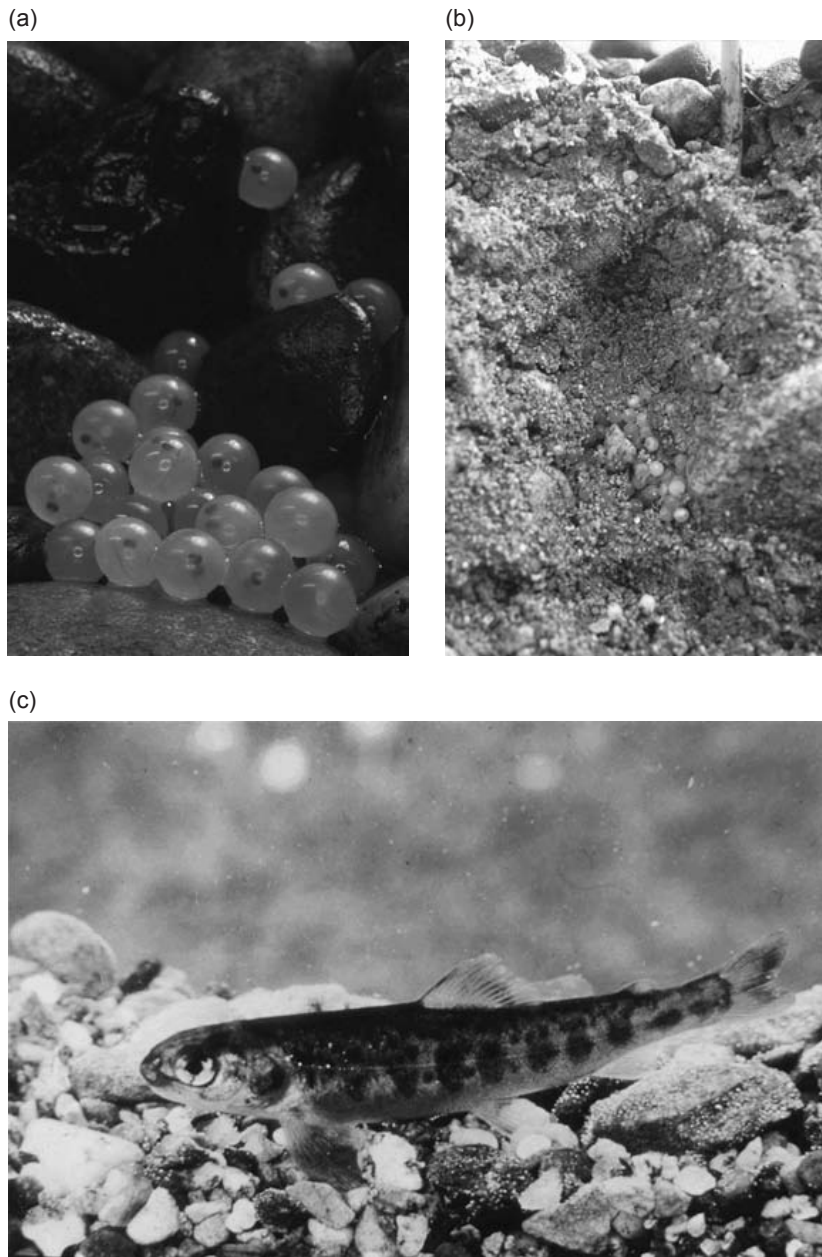


Figure 1.4. (a) Eggs, (b) a nest, and (c) a juvenile Atlantic salmon – stars of the computation of Einum and Fleming on optimal egg size. Photos compliments of Ian Fleming and Neil Metcalfe.

and we can find the optimal egg size by setting the derivative of $R(g, x)$ with respect to x equal to 0 and solving for x .

Exercise 1.4 (M)

Show that the optimal egg size based on Eq. (1.8) is $x_{\text{opt}} = \{c(a + 1)\}^{1/a}$ and for the values from Einum and Fleming that this is 0.1244 g. For comparison, the observed egg size in their experiments was about 0.12 g.

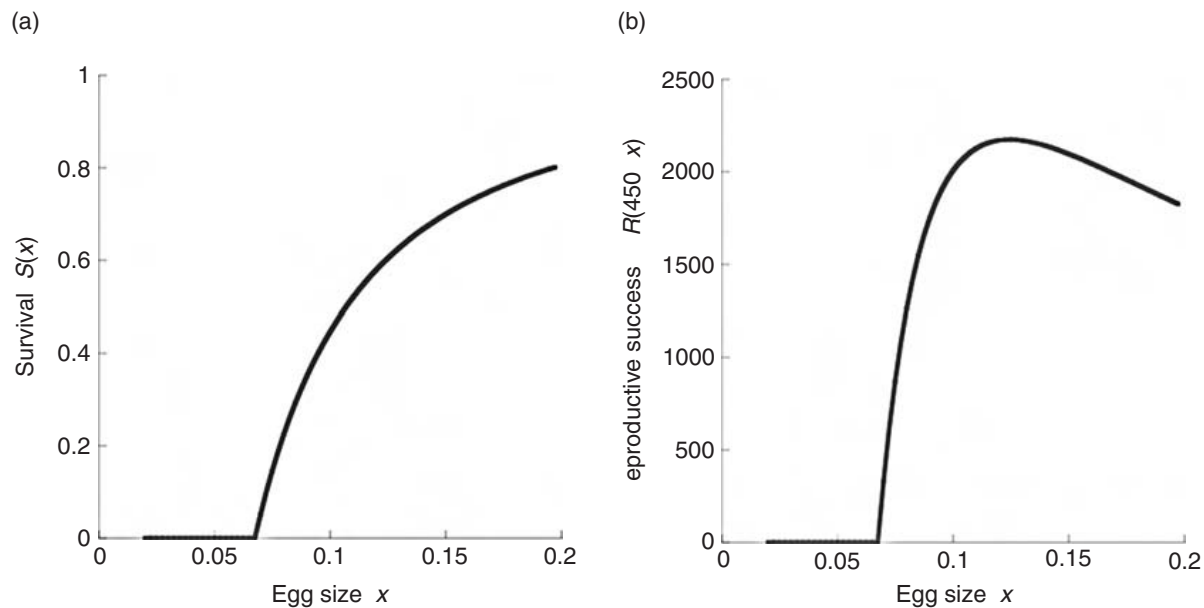


Figure 1.5. (a) Offspring survival as a function of egg mass for Atlantic salmon. (b) Female reproductive success for an individual with 450 g of gonads.

In Figure 1.5b, I show $R(450, x)$ as a function of x ; we see the peak very clearly. We also see a source of parent–offspring conflict: from the perspective of the mother, an intermediate egg size is best – individual offspring have a smaller chance of survival, but she is able to make more of them. Since she is making the eggs, this is a case of parent–offspring conflict that the mother wins with certainty.

A calculation similar to this one was done by Heath *et al.* (2003), in their study of the evolution of egg size in Atlantic salmon.

Extraordinary sex ratio (more calculus)

We now turn to one of the most important contributions to evolutionary biology (and ecology) in the last half of the twentieth century; this is the thinking by W. D. Hamilton leading to understanding extraordinary sex ratios. There are two starting points. The first is the argument by R. A. Fisher that sex ratio should generally be about 50:50 (Fisher 1930): imagine a population in which the sex ratio is biased, say towards males. Then an individual carrying genes that will lead to more daughters will have higher long term representation in the population, hence bringing the sex ratio back into balance. The same argument applies if the sex ratio is biased towards females. The second starting point is the observation that in many species of insects, especially the parasitic wasps (you’ll see some pictures of these animals in Chapter 4), the

sex ratio is highly biased towards females, in apparent contradiction to Fisher's argument.

The parasitic wasps are wonderfully interesting animals and understanding a bit about their biology is essential to the arguments that follow. If you find this brief description interesting, there is no better place to look for more than in the marvelous book by Charles Godfray (Godfray 1994). In general, the genetic system is haplo-diploid, in which males emerge from unfertilized eggs and females emerge from fertilized eggs. Eggs are laid on or in the eggs, larvae or adults of other insects; the parasitoid eggs hatch, offspring burrow into the host if necessary, and use the host for the resources necessary to complete development. Upon completing development, offspring emerge from the wreck that was once the host, mate and fly off to seek other hosts and the process repeats itself. In general, more than one, and sometimes many females will lay their eggs at a single host. Our goal is to understand the properties of this reproductive system that lead to sex ratios that can be highly female biased.

Hamilton's approach (Hamilton 1967) gave us the idea of an "unbeatable" or non-invadable sex ratio, from which many developments in evolutionary biology flowed. The paper is republished in a book that is well worth owning (Hamilton 1995) because in addition to containing 15 classic papers in evolutionary ecology, each paper is preceded by an essay that Hamilton wrote about the paper, putting it in context.

Imagine a population that consists of $N + 1$ individuals, who are identical in every way except that N of them (called "normal" individuals) make a fraction of sons r^* and one of them (called the "mutant" individual) makes a fraction of sons r . We will say that the normal sex ratio r^* is unbeatable if the best thing that the mutant can do is to adopt the same strategy herself. (This is an approximate definition of an Evolutionarily Stable Strategy (ESS), but misses a few caveats – see [Connections](#)). To find r^* , we will compute the fitness of the mutant given both r and r^* , then choose the mutant strategy appropriately.

In general, fitness is measured by the long term number of descendants (or more specifically the genes carried by them). As a proxy for fitness, we will use the number of grand offspring produced by the mutant female (grand offspring are a convenient proxy in this case because once the female oviposits and leaves a host, there is little that she can do to affect the future representation of her genes).

A female obtains grand offspring from both her daughters and her sons. We will assume that all of the daughters of the mutant female are fertilized, that her sons compete with the sons of normal females for

matings, and that every female in the population makes E eggs. Then the number of daughters made by the mutant female is $E(1-r)$ and the number of grand offspring from these daughters is $E^2(1-r)$. Similarly, the total number of daughters at the host will be $E(1-r) + NE(1-r^*)$, so that the number of grand offspring from all daughters is $E^2\{1-r + N(1-r^*)\}$. However, the mutant female will be credited with only a fraction of those offspring, according to the fraction of her sons in the population. Since she makes Er sons and the normal individuals make NEr^* sons, the fraction of sons that belong to the mutant is $Er/(Er + NEr^*)$. Consequently, the fitness $W(r, r^*)$, depending upon the sex ratio r that the female uses and the sex ratio r^* that other females use, from both daughters and sons is

$$W(r, r^*) = E^2(1-r) + E^2\{(1-r) + N(1-r^*)\} \left[\frac{r}{r + Nr^*} \right] \quad (1.9)$$

The strategy r^* will be “unbeatable” (or “uninvadable”) if the best sex ratio for the mutant to choose is r^* ; as a function of r , $W(r, r^*)$ is maximized when $r=r^*$. We thus obtain a procedure for computing the unbeatable sex ratio: (1) take the partial derivative of $W(r, r^*)$ with respect to r ; (2) set $r=r^*$ and the derivative equal to 0; and (3) solve for r^* .

Exercise 1.5 (M)

Show that the unbeatable sex ratio is $r^* = N/2(N+1)$.

Let us interpret this equation. When $N \rightarrow \infty$, $r^* \rightarrow 1/2$; this is understandable and consistent with Fisherian sex ratios. As the population becomes increasingly large, the assumptions underlying Fisher’s argument are met. How about the limit as $N \rightarrow 0$? Formally, the limit as $N \rightarrow 0$ is $r^* = 0$, but this must be biologically meaningless. When $N = 0$, the mutant female is the only one ovipositing at a host. If she makes no sons, then none of her daughters will be fertilized. How are we to interpret the result? One way is this: if she is the only ovipositing female, then she is predicted to lay enough male eggs to ensure that all of her daughters are fertilized (one son may be enough). To be sure, there are lots of biological details missing here (see [Connections](#)), but the basic explanation of extraordinary sex ratios has stood the test of time.

Two metaphors

You should be warmed up now, ready to begin the serious work. Before doing so, I want to share two metaphors about the material in this book.

Black and Decker

Black and Decker is a company that manufactures various kinds of tools. In Figure 1.6, I show some of the tools of my friend Marv Guthrie, retired Director of the Patent and Technology Licensing Office at Massachusetts General Hospital and wood-worker and sculptor. Notice that Marv has a variety of saws, pliers, hammers, screwdrivers and the like. We are to draw three conclusions from this collection. First, one tool cannot serve all needs; that is why there are a variety of saws, pliers, and screwdrivers in his collection. (Indeed, many of you probably know the saying “When the only tool you have is a hammer, everything looks like a nail”.) Similarly, we need a variety of tools in ecology and evolutionary biology because one tool cannot solve all the problems that we face.

Second, if you know how to use one kind of screwdriver, then you will almost surely understand how other kinds of screwdrivers are used. Indeed, somebody could show a new kind of screwdriver to you, and you would probably be able to figure it out. Similarly, the goal in this book is not to introduce you to every tool that could be used in ecology and evolutionary biology. Rather, the point is to give you enough understanding of key tools so that you can recognize (and perhaps develop) other ones.

Third, none of us has envisioned all possible uses of any tool – but understanding how a tool is used allows us to see new ways to use it. The same is true for the material in this book: by deeply understanding some of the ways in which these tools are used, you will be able to discover new ways to use them. So, there will be places in the book where I will



Figure 1.6. The tools of my friend Marv Guthrie; such tools are one metaphor for the material in this book.

set up a situation in which a certain tool could be used, but will not go into detail about it because we've already have sufficient exposure to that tool (sufficient, at least for this book; as with physical tools, the more you use these tools, the better you get at using them).

Fourth, a toolbox does not contain every possible tool. The same is true of this book – a variety of tools are missing. The main tools missing are game theoretical methods and partial differential equation models for structured populations. Knowing what is in here well, however, will help you master those tools when you need them.

There is one tool that I will not discuss in detail but which is equally important: what applies to mathematical methods also applies to writing, once you have used the methods to solve a problem. The famous statistician John Hammersley (Hammersley 1974), writing about the use of statistics in decision-making and about statistical professionalism says that the art of statistical advocacy “resides in one particular tool, which we have not yet mentioned and which we too often ignore in university courses on statistics. The tool is a clear prose style. It is, without any doubt, the most important tool in the statistician’s toolbox” (p. 105). Hammersley offers two simple rules towards good prose style: (1) use short words, and (2) use active verbs. During much of the time that I was writing the first few drafts of this book, I read the collected short stories of John Cheever (Cheever 1978) and it occurred to me that writers of short stories face the same problems that we face when writing scientific papers: in the space of 10 or so printed papers, we need to introduce the reader to a world that he or she may not know about and make new ideas substantial to the reader. So, it is probably good to read short stories on a regular basis; the genre is less important. Cheever, I might add, is a master of using simple prose effectively, as is Victor Pritchett (Pritchett 1990a, b).

In his book *On Writing* (King 2000), Stephen King has an entire section called “Toolbox”, regarding which he says “I want to suggest that to write to the best of your abilities, it behooves you to construct your own toolbox and then build up enough muscle so that you can carry it with you. Then, instead of looking at a hard job and getting discouraged, you will perhaps seize the correct tool and get immediately to work” (p. 114). King also encourages everyone to read the classic *Elements of Style* (Strunk and White 1979) by William Strunk and E. B. White (of *Charlotte’s Web* and *Stuart Little* fame). I heartily concur; if you think that you ever plan to write science – or anything for that matter – you should own Strunk and White and re-read it regularly. One of my favorite authors of fiction, Elizabeth George, has a lovely small book on writing (George 2004) and emphasizes the same when she writes: “that the more you know about your tools, the better

you'll be able to use them" (p. 158). She is speaking about the use of words; the concept is more general.

Almost everyone reading this book will be interested in applying mathematics to a problem in the natural world. Skorokhod *et al.* (2002) describe the difference between pure and applied mathematics as this: "This book has its roots in two different areas of mathematics: pure mathematics, where structures are discovered in the context of other mathematical structures and investigated, and applications of mathematics, where mathematical structures are suggested by real-world problems arising in science and engineering, investigated, and then used to address the motivating problem. While there are philosophical differences between applied and pure mathematical scientists, it is often difficult to sort them out." (p. v).

In order to apply mathematics, you must be engaged in the world. And this means that your writing must be of the sort that engages those who are involved in the real world. Some years ago, I co-chaired the strategic planning committee for UC Santa Cruz, sharing the job with a historian, Gail Hershatter, who is a prize winning author (Hershatter 1997). We agreed to split the writing of the first draft of the report evenly and because I had to travel, I sent my half to her before I had seen any of her writing. I did this with trepidation, having heard for so many years about C. P. Snow's two cultures (Snow 1965). Well, I discovered that Gail's writing style (like her thinking style) and mine were completely compatible. She and I talked about this at length and we agreed that there are indeed two cultures, but not those of C. P. Snow. There is the culture of good thinking and good writing, and the culture of bad thinking and bad writing. And as we all know from personal experience, they transcend disciplinary boundaries. As hard as you work on mathematical skills, you need to work on writing skills. This is only done, Stephen King notes, by reading widely and constantly (and, of course, in science we never know from where the next good idea will come – so read especially widely and attend seminars).

Mean Joe Green

The second metaphor involves Mean Joe Green. At first, one might think that I intend Mean Joe Greene, the hall of fame defensive tackle for the Pittsburgh Steelers (played 1968–1981), although he might provide an excellent metaphor too. However, I mean the great composer of opera Giuseppe Verdi (lived 1813–1901; Figure 1.7).

Opera, like the material in this book, can be appreciated at many levels. First, one may just be surrounded by the music and enjoy it, even if one does not know what is happening in the story. Or, one may know

Figure 1.7. The composer G. Verdi, who provides a second metaphor for the material in this book. This portrait is by Giovanni Boldini (1886) and is found in the Galleria Comunale d'Arte Moderna in Rome. Reprinted with permission.



the story of the opera but not follow the libretto. One may sit in an easy chair, libretto open and follow the opera. Some of us enjoy participating in community opera. Others aspire to professional operatic careers. And a few of us want to be Verdi. Each of these – including the first – is a valid appreciation of opera.

The material in this book does not come easily. I expect that readers of this book will have different goals. Some will simply desire to be able to read the literature in theoretical biology (and if you stick with it, I promise that you will be able to do so by the end), whereas others will desire different levels of proficiency at research in theoretical biology. This book will deliver for you too.

Regardless of the level at which one appreciates opera, one key observation is true: you cannot say that you've been to the opera unless you have been there. In the context of quantitative methods, working through the details is the only way to be there. From the perspective of the author, it means writing a book that rarely has the phrase "it can be shown" (implying that a particular calculation is too difficult for the reader) and for the reader it means putting the time in to do the problems. All of the exercises given here have been field tested on graduate students at the University of California Santa Cruz and elsewhere. An upper division undergraduate student or a graduate student early in his or her career can master all of these exercises with perseverance – but even the problems marked E may not be easy enough to do quickly in front of the television or in a noisy café. Work through these problems, because they will help you develop intuition. As Richard Courant once noted, if we get the intuition right, the details will follow (for more about Courant, see Reid (1976)). Our goal is to build intuition about biological systems using the tools that mathematics gives to us.

The population biology of disease is one of the topics that we will cover, and Verdi provides a metaphor in another way, too. In a period of about two years, his immediate family (wife, daughter and son) were felled by infectious disease (Greenberg 2001). For more about Verdi and his wonderful music, see Holden (2001), Holoman (1992) or listen to Greenberg (2001).

How to use this book (how I think you got here)

I have written this book for anyone (upper division undergraduates, graduate students, post-docs, and even those beyond) who wants to develop the intuition and skills required for reading the literature in theoretical and mathematical biology and for doing work in this area. Mainly, however, I envision the audience to be upper division and first or second year graduate students in the biological sciences, who want to learn the right kind of mathematics for their interests. In some sense, this is the material that I would like my Ph.D. students to deeply know and understand by the middle of their graduate education. Getting the skills described in this book – like all other skills – is hard but not impossible. As I mentioned above, it requires work (doing the exercises). It also requires returning to the material again and again (so I hope that your copy of this book becomes marked up and well worn); indeed, every time I return to the material, I see it in new and deeper ways and gain new insights. Thus, I hope that colleagues who are already expert in this subject will find new ways of seeing their own problems from reading the book. Siwoff *et al.* (1990) begin their book with “Flip through these pages, and you’ll see a book of numbers. Read it, and you’ll realize that this is really a book of ideas. Our milieu is baseball. Numbers are simply our tools” (p. 3). A similar statement applies to this book: we are concerned with ideas in theoretical and mathematical biology and equations are our tools.

Motivated by the style of writing by Mike Rosenzweig in his book on diversity (Rosenzweig 1995), I have tried to make this one fun to read, or at least as much fun as a book on mathematical methods in biology can be. That’s why, in part, I include pictures of organisms and biographical material.

I taught all of the material, except the chapter on fisheries, in this book as a six quarter graduate course, meeting once a week for two hours a time. I also taught the material on differential equations and disease in a one quarter formal graduate course meeting three times a week, slightly more than an hour each time; I did the same with the two chapters on stochastic population theory. The chapter on fisheries is

based on a one quarter upper division/graduate class that met twice a week for about two hours.

Connections

In an effort to keep this book of manageable size, I had to forgo making it comprehensive. Much of the book is built around current or relatively current literature and questions of interest to me at the timing of writing. Indeed, once we get into the particular applications, you will be treated to a somewhat idiosyncratic collection of examples (that is, stuff which I like very much). It is up to the reader to discover ways that a particular tool may fit into his or her own research program. At the same time, I will end each chapter with a section called **Connections** that points towards other literature and other ways in which the material is used.

The marginal value theorem

There are probably more than one thousand papers on each of the marginal value theorem, the two prey diet choice problem, parent–offspring conflict, and extraordinary sex ratios. These ideas represent great conceptual advances and have been widely used to study a range of questions from insect oviposition behavior to mate selection; many of the papers add different aspects of biology to the models and investigate the changes in predictions. These theories also helped make behavioral ecology a premier ecological subject in which experiments and theory are linked (in large part because the scale of both theory and observation or experiment match well). At the same time, the ability to make clear and definitive predictions led to a long standing debate about theories and models (Gray 1987, Mitchell and Valone 1990), and what differences between an experimental result and a prediction mean. Some of these philosophical issues are discussed by Hilborn and Mangel (1997) and a very nice, but brief, discussion is found in the introduction of Dyson (1999). The mathematical argument used in the marginal value theorem is an example of a renewal process, since the foraging cycle “renews” itself every time. Renewal processes have a long and rich history in mathematics; Lotka (of Lotka–Volterra fame) worked on them in the context of population growth.

Unbeatable and evolutionarily stable strategies

The notion of an unbeatable strategy leads us directly to the concept of evolutionarily stable strategies and the book by John Maynard Smith (1982) is still an excellent starting point; Hofbauer and Sigmund (1998)

and Frank (1998) are also good places to look. Hines (1987) is a more advanced treatment and is a monograph in its own right. In this paper, Hines also notes that differences between the prediction of a model and the observations may be revealing and informative, showing us (1) that the model is inadequate and needs to be improved, (2) the fundamental complexity of biological systems, or (3) an error in the analysis.

On writing and the creative process

In addition to Strunk and White, I suggest that you try to find Robertson Davies's slim volume called *Reading and Writing* (Davies 1992) and get your own copy (and read and re-read it) of William Zinsser's *On Writing Well* (Zinsser 2001) and *Writing to Learn* (Zinsser 1989). You might want to look at Highman (1998), which is specialized about writing for the mathematical sciences, as well. In his book, Davies notes that it is important to read widely – because if you read only the classics, how do you know that you are reading the classics? There is a wonderful, and humorous, piece by Davis and Gregerman (1995) in which this idea is formalized into the quanta of flawedness in a scientific paper (which they call phi) and the quantum of quality (nu). They suggest that all papers should be described as $X:Y$, where X is the quanta of phi and Y is the quanta of nu. There is some truth in this humor: whenever you read a paper (or hear a lecture) ask what are the good aspects of it, which you can adapt for your own writing or oral presentations. The interesting thing, of course, is that we all recognize quality but at the same time have difficulty describing it. This is the topic that Prisig (1974) wrestles with in *Zen in the Art of Motorcycle Maintenance*, which is another good addition to your library and is in print in both paperback and hardback editions. In his book, Stephen King also discusses the creative process, which is still a mystery to most of the world (that is – just how do we get ideas). A wonderful place to start learning about this is in the slim book by Jacques Hadamard (1954), who was a first class mathematician and worried about these issues too.