# 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

Cambridge University Press
0521830451 - The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology
Marc Mangel
Excerpt
More information

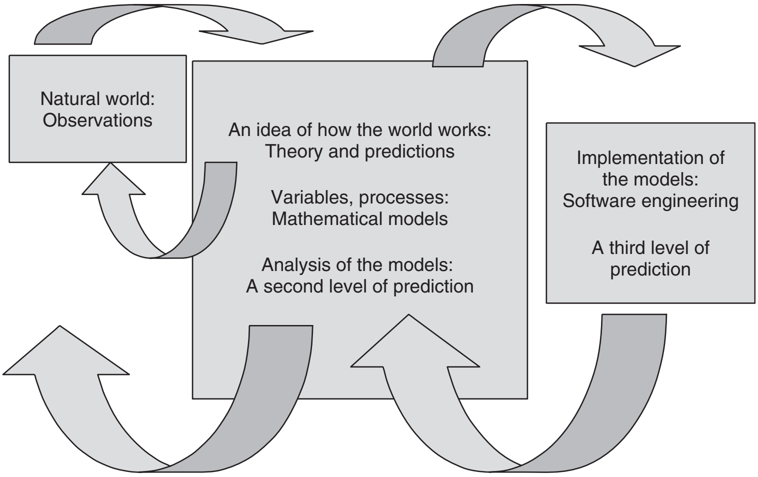

**Figure 1.1.** Theoretical biology begins with the natural world, which we want to understand. By thinking about observations of the world, we begin to conceive an idea about how it works. This is theory, and may already lead to predictions, which can then flow back into our observations of the world. 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

© Cambridge University Press

CAMBRIDGE

Cambridge University Press
0521830451 - The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology
Marc Mangel
Excerpt
More information

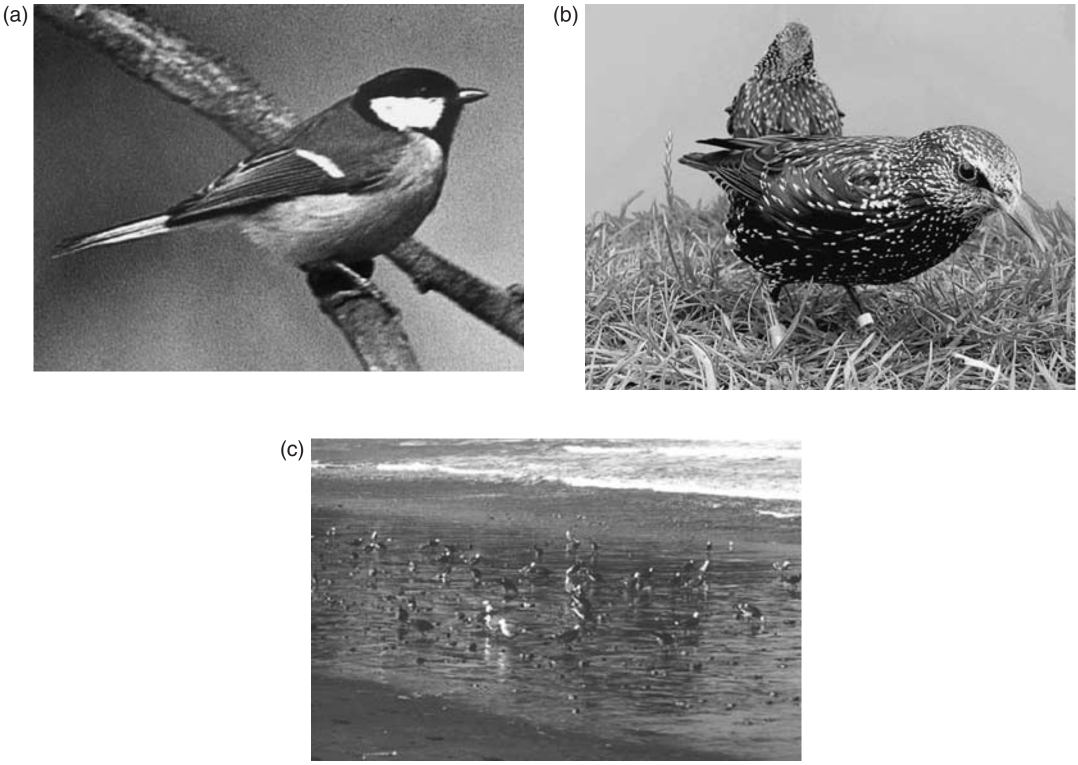

**Figure 1.2.** Two stars of foraging experiments are (a) the great tit, *Parus major*, and (b) the common starling *Sturnus vulgaris* (compliments of Alex Kacelnik, University of Oxford). (c) Foraging seabirds on New Brighton Beach, California, face diet choice and patch leaving problems.

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 $\lambda_i$ 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

© Cambridge University Press www.cambridge.org

CAMBRIDGE

Cambridge University Press
0521830451 - The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology
Marc Mangel
Excerpt
More information

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

$$T = S + h_1\lambda_1 S = S(1 + \lambda_1 h_1) \tag{1.1}$$

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

$$S = \frac{T}{1 + \lambda_1 h_1} \tag{1.2}$$

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

$$R_s = \frac{E_1\lambda_1}{1 + h_1\lambda_1} \tag{1.3}$$

## 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

CAMBRIDGE

Cambridge University Press
0521830451 - The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology
Marc Mangel
Excerpt
More information

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

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

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

$$\lambda_1 > \frac{E_2}{E_1h_2 - E_2h_1} \tag{1.5}$$

Equation (1.5) defines a "switching value" for the encounter rate with the more profitable prey item, since as $\lambda_1$ 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

© Cambridge University Press www.cambridge.org

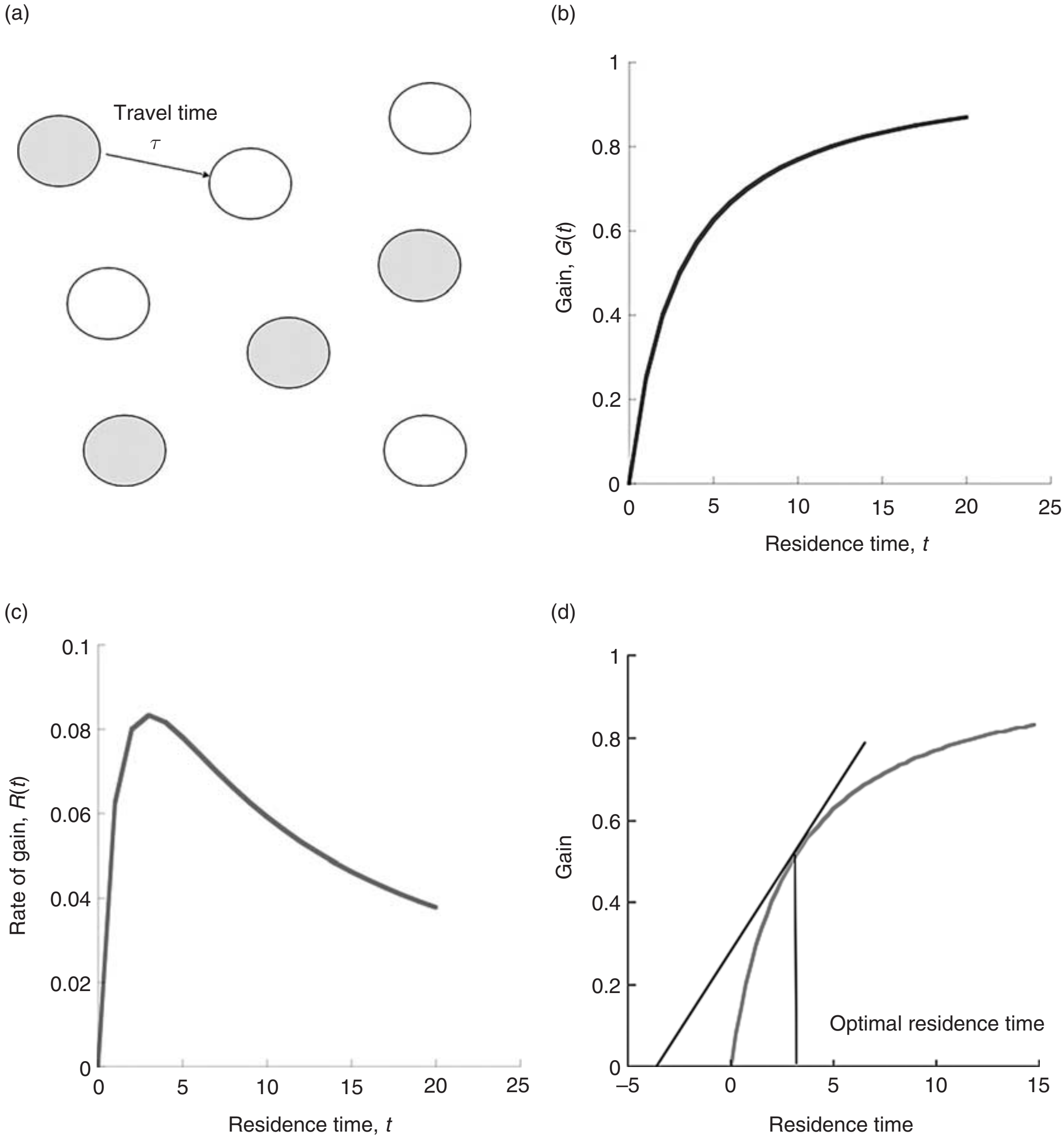

**Figure 1.3.** (a) A schematic of the situation for which the marginal value theorem applies. Patches of food (represented here in metaphor by filled or empty patches) are exhaustible (but there is a very large number of them) and separated by travel time $\tau$. (b) An example of a gain curve (here 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.

CAMBRIDGE

Cambridge University Press
0521830451 - The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology
Marc Mangel
Excerpt
More information

(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 $\tau$. 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 $\tau$ 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

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

CAMBRIDGE

Cambridge University Press
0521830451 - The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology
Marc Mangel
Excerpt
More information

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

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

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

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

© Cambridge University Press www.cambridge.org

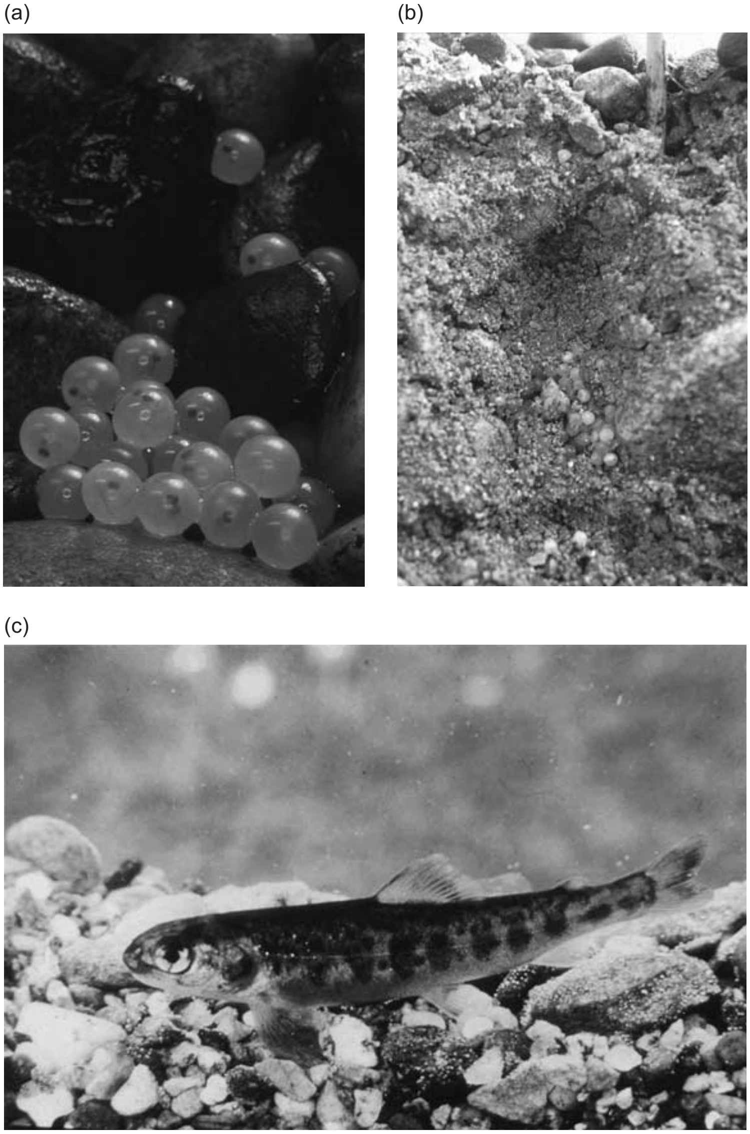

**Figure 1.4.** (a) Eggs, (b) a nest, and (c) a juvenile Atlantic salmon – stars of the computation of Einum and Fleming on optimal egg size. Photos complements of Ian Fleming and Neil Metcalfe.

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 $x_{\mathrm{opt}} = \{c(a+1)\}^{1/a}$ 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.

Cambridge University Press
0521830451 - The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology
Marc Mangel
Excerpt
More information

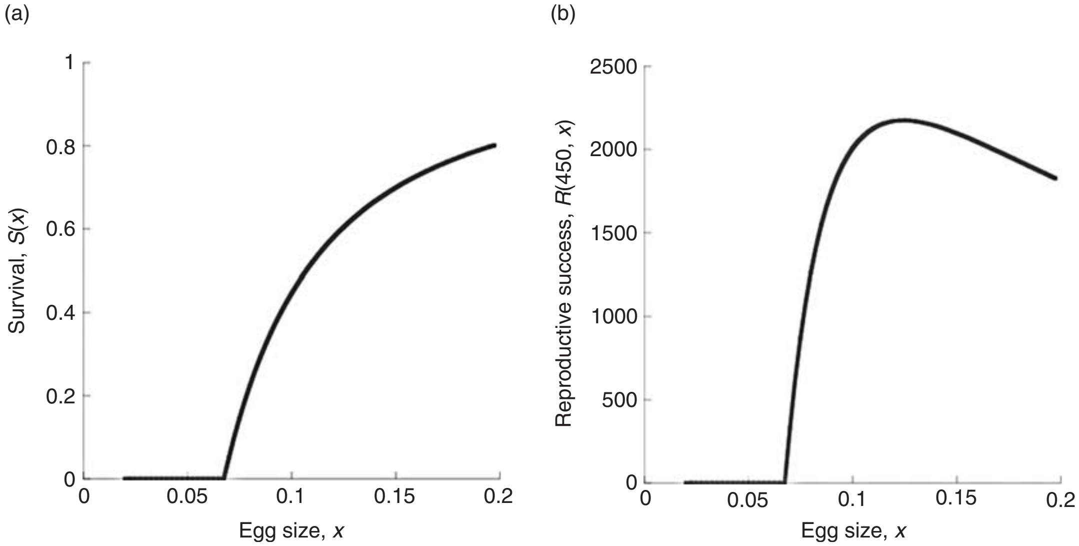

**Figure 1.5.** (a) Offspring survival as a function of egg mass for Atlantic salmon. (b) Female reproductive success for an individual with 450 g of gonads.

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

© Cambridge University Press