Chapter 2

Optimality Models

Natural selection leads to the evolution of traits that yield higher **fitness** or **reproductive success**. Traits that yield the highest fitness among all possibilities are **optimal**.

We begin, in this chapter, by describing how to construct an **optimality model**, that is, a mathematical model that allows us to determine the optimal trait in a set of possibilities. Our approach is based on worked examples: we will focus on the evolution of parental care, and of foraging behaviour. The models we present, although simple, serve to illustrate the key steps in the construction of any optimality model.

2.1 Parental Care

The purpose of our first illustrative model is to explore the selective pressures that favour parental care of offspring, as opposed to desertion of the current mate and young in order to seek new mating partners.

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2.1.1   Choosing a strategy set

The first step in building an optimality model is to define the ***strategy set***, *i.e.,* the range of possible traits or behaviours available to selection. Only then can we go on to determine the 'best' or optimal member(s) of the set.

The strategy set may be discrete or continuous. A discrete set contains a countable number of distinct alternatives; in the simplest case, there may be just two possibilities. For instance, a simple model of parental care might allow for only two alternative strategies: care or desert. A more complex model might, by contrast, allow for variation in the duration of care. The model would then feature a continuous strategy set, including all possible, non-negative values of t, the time for which a parent will remain to look after its current brood of offspring.

As the above example illustrates, there is often more than one way to build an optimality model of the same trait or behaviour. How then do we decide what range of strategies to consider? There is no simple answer to this question. On the one hand, we need to bear in mind the technical challenge of analysing the model. The greater the range of strategies under consideration, the harder it is likely to be to identify an optimal solution. So a simple model that allows for only a few alternatives, such as the decision to care or desert, is often a good starting point for analysis. On the other hand, a wider range of possible strategies may better reflect the complexity of the real world.

Ultimately, the choice of strategy set depends upon our intuition as to what is biologically plausible. For instance, we assumed above that a parent must *either* care for the current brood of offspring *or* desert them in search of a new mate. But in some species, these options need not prove mutually exclusive. A parent who cares for its offspring may defend a territory or nest to which it can attract additional partners; under these circumstances, we would have to allow for the possibility of courting new mates without abandoning the current brood of young.

2.1.2   Specifying a currency

Once we have decided upon the strategy set, the second step in building a model is to specify the optimisation criterion, or ***currency***. This is the criterion that we will use to compare alternative strategies, and to identify the 'best' one.

There are many different currencies that we might use, depending on the kind of trait or behaviour we are dealing with. In the case of our parental care example, it is natural to compare alternative strategies in terms of the expected reproductive success that they yield. The 'best' strategy (which will be favoured by selection) is the one that leads to the production of the greatest number of surviving offspring.

In other cases, however, it is hard to measure the success of different strategies in these terms. We would then have to use an alternative optimisation criterion that is easier to assess, as a proxy for fitness or reproductive success. To compare alternative foraging strategies, for instance, we might focus on the average rate of food intake that each strategy yields, or the risk of starvation over some period of time. We would then identify the best strategy as the one that maximises intake rate, or minimises starvation risk (assuming that a greater intake rate or reduced starvation risk will lead to greater fitness).

As with the choice of a strategy set, which currency we specify is largely a matter of biological intuition. To choose one currency rather than another is to make an assumption about which selective pressures are most important in a given situation. The model we build cannot prove that our choice of currency is appropriate. It merely allows us to deduce what predictions follow from our assumption(s).

2.1.3 Calculating payoffs

Once we have chosen a strategy set, and specified a currency for optimisation, it is time to determine the **payoff** that each strategy yields. In other words, we must assess the consequences of each strategy for an individual that adopts it, in terms of the currency we have chosen.

Each course of action will usually entail a variety of costs and benefits, the magnitude of which will vary from one species or situation to another. To quantify these costs and benefits, we will need to specify corresponding model parameters. Between them, the parameters we specify must determine the precise consequences of each possible strategy.

To see how this works, we can return to the evolution of parental care. For simplicity, let us consider the basic model described above, featuring a discrete strategy set with only two possible alternatives: care or desert. Our optimisation criterion is reproductive success, *i.e.,* the total number of surviving young that an individual produces.

What are the costs and benefits (in terms of reproductive success) of desertion vs. care? On the one hand, the survival prospects of a parent's current brood of offspring are likely to be reduced if it deserts them. On the other hand, if it does desert, the parent may have a chance to find a new mate and produce a second brood (while if it stays to care for its young, we will assume that it cannot mate again).

To quantify these costs and benefits, we must specify several parameters:

- n, the number of offspring in a brood

- s_C, the proportion of offspring that survive from the current brood if the parent cares

- s_D, the proportion of offspring that survive from the current brood if the parent deserts

- m, the probability that a parent who deserts will find a second mate

- s_L, the proportion of later-born offspring that survive from a second brood

Having specified these parameters, we can write down the payoffs (in terms of the expected number of surviving offspring) to a parent who cares and to a parent who deserts, which we will denote $W(\text{Care})$ and $W(\text{Desert})$. W is the **payoff function**[1]. A parent who cares produces n offspring in the current brood, of whom a proportion s_C survive, so

$$W(\text{Care}) = ns_C \tag{2.1}$$

A parent who deserts produces n offspring in the current brood, of whom a proportion s_D survive. In addition, with probability m the parent finds a second mate, with whom it produces an additional brood of n offspring, of whom a proportion s_L survive (we define a new parameter for the survival of offspring from a second brood, because later-born young may have poorer prospects). So, overall

$$W(\text{Desert}) = ns_D + mns_L = n(s_D + ms_L) \tag{2.2}$$

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[1]Throughout this book we will use W to denote payoff functions.

2.1.4 Identifying optimal strategies

Now that we have calculated the payoffs to care and to desertion, we can 'solve' the model by determining when selection will (and when it will not) favour parental care. A parent does best to stay and care for its young if and only if the payoff to doing so is greater than the payoff to desertion, *i.e.,* if and only if

$$W(\text{Care}) > W(\text{Desert}) \tag{2.3}$$

If we substitute into inequality (2.3) the expressions for $W(\text{Care})$ and $W(\text{Desert})$ given in equations (2.1) and (2.2), we find that selection will favour parental care if and only if

$$ns_\text{C} > n(s_\text{D} + ms_\text{L}) \tag{2.4}$$

We can cancel the term n from both sides of this inequality, yielding

$$s_\text{C} > s_\text{D} + ms_\text{L} \tag{2.5}$$

and rearrange to obtain the following simple condition

$$m < \frac{s_\text{C} - s_\text{D}}{s_\text{L}} \tag{2.6}$$

We will interpret this inequality biologically in §2.1.5 below.

For future reference, it will be useful to make precise what we mean by an optimal strategy, and to distinguish cases where there is a unique optimal solution to a model.

Definition 1 (Optimal Strategy). *Given a strategy set $\mathcal{S}$ and a payoff function $W(s)$, a strategy $\hat{s}$ is said to be **optimal** if and only if $W(\hat{s}) \geq W(s)$ for each $s \in \mathcal{S}$ and **strictly optimal** if and only if $W(\hat{s}) > W(s)$ for each $s \in \mathcal{S}, s \neq \hat{s}$.*

Note that while there can be several optimal strategies (each equally good), if there is a strictly optimal strategy then it is unique for a given model.

2.1.5 Generating predictions

What does condition (2.6) tell us? Parental care will be favoured if and only if m, the probability of finding a new mate following desertion, is less than some critical value that depends upon s_C, s_D and s_L. In other words, as we

might expect, a parent is more likely to stay and care if there is little chance of remating, but more likely to desert if it is easy to find a new partner.

We can be more precise than this, however. The right hand side of condition (2.6) represents the increase in offspring survival if a parent stays to care for its young ($s_\mathrm{C} - s_\mathrm{D}$), relative to the survival of offspring from a second brood (s_L). So we can summarise the predictions of the model as follows: a parent does best to care if and only if the probability of remating after desertion is less than the increase in offspring survival due to care, relative to the survival of a second brood. Put another way, caring is the optimal strategy if the incremental benefit of caring for a first brood outweighs the benefit of producing a second brood.

For easy reference, we will list the assumptions and solution of this model (and of all the subsequent models we describe), in a 'model summary' box.

MODEL SUMMARY 2.1 – Parental care 1

Model type: discrete optimality model

Strategy set: {Care, Desert}

Currency: expected reproductive success

Model notation:

n, brood size

s_{C}, survival of current brood if parent cares

s_{D}, survival of current brood if parent deserts

m, probability of remating following desertion

s_{L}, survival of later-born young

Payoffs:

$W(\mathrm{Care}) = ns_{\mathrm{C}}$

$W(\mathrm{Desert}) = n(s_{\mathrm{D}} + ms_{\mathrm{L}})$

Optimal solutions:

$m < \frac{s_{\mathrm{C}} - s_{\mathrm{D}}}{s_{\mathrm{L}}}$: Care

$m = \frac{s_{\mathrm{C}} - s_{\mathrm{D}}}{s_{\mathrm{L}}}$: Care or Desert

$m > \frac{s_{\mathrm{C}} - s_{\mathrm{D}}}{s_{\mathrm{L}}}$: Desert

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2.2 Prey choice

Having worked through our first optimality model, we can use a similar approach to investigate other kinds of behaviour, such as foraging. Consider a predator that encounters two types of prey while searching for food. Both types require the same amount of time, t_{h}, to handle (*i.e.*, to capture and consume). However, 'fat' prey items are of relatively high energetic value, v_{F}, and 'lean' items of relatively low value, v_{L} ($< v_{\mathrm{F}}$). Fat prey are encountered at rate E_{F} and lean prey at rate E_{L} (*i.e.*, for every unit of time spent searching, the predator encounters on average E_{F} fat prey and E_{L} lean prey).

167   What is the optimal diet for the predator?

2.2.1   Strategy set

We will consider two alternative strategies: 'Specialist' and 'Generalist'. A specialist predator will attack only fat prey (and will ignore lean items), whereas a generalist predator will take both prey types.

2.2.2   Currency

Our currency will be the long-term average rate of energy intake.

2.2.3   Payoffs

Consider, first, a specialist predator. For every t_s units of time spent searching, it encounters on average $t_s E_F$ fat prey items, and expends a time of $t_s E_F t_h$ handling them. From these items, it obtains a total energetic yield of $t_s E_F v_F$. Any lean prey that the predator runs into are simply ignored. The predator thus gains an average yield of $t_s E_F v_F$ for an average total time expenditure (on searching and handling) of $t_s + t_s E_F t_h$. The long-term average rate of energy gain for a specialist, which we denote $W(\text{Specialist})$, is thus

$$W(\text{Specialist}) = \frac{t_s \, E_F \, v_F}{t_s + t_s \, E_F \, t_h} \tag{2.7}$$

and we can cancel out t_s to obtain

$$W(\text{Specialist}) = \frac{E_F \, v_F}{1 + E_F \, t_h} \tag{2.8}$$

What about a generalist predator? For every t_s units of time spent searching, it encounters on average $t_s E_F$ fat prey and $t_s E_L$ lean prey. It expends a total time of $t_s E_F t_h + t_s E_L t_h$ handling these prey, and gains a total energetic yield of $t_s E_F v_F + t_s E_L v_L$ from them. The generalist predator's long term average rate of energy intake, $W(\text{Generalist})$ is thus

$$W(\text{Generalist}) = \frac{t_s \, E_F \, v_F + t_s \, E_L \, v_L}{t_s + t_s \, E_F \, t_h + t_s \, E_L \, t_h} \tag{2.9}$$

and we can once again cancel out t_s, which gives us

$$W(\text{Generalist}) = \frac{E_F \, v_F + E_L \, v_L}{1 + E_F \, t_h + E_L \, t_h} \tag{2.10}$$

2.2.4   Optimal strategy

Which is the optimal strategy? Selection will favour generalist predators if and only if

$$W(\text{Generalist}) > W(\text{Specialist}) \tag{2.11}$$

Making use of the expressions we have derived for these terms, we can write this condition as

$$\frac{E_{\text{F}}\, v_{\text{F}} + E_{\text{L}}\, v_{\text{L}}}{1 + E_{\text{F}}\, t_{\text{h}} + E_{\text{L}}\, t_{\text{h}}} > \frac{E_{\text{F}}\, v_{\text{F}}}{1 + E_{\text{F}}\, t_{\text{h}}} \tag{2.12}$$

We could stop here, but with a bit of ingenuity, we can simplify this condition in an enlightening way. First, if we multiply both sides of the inequality by the denominator of the left hand side we obtain

$$E_{\text{F}}\, v_{\text{F}} + E_{\text{L}}\, v_{\text{L}} > E_{\text{F}}\, v_{\text{F}} \left(\frac{1 + E_{\text{F}}\, t_{\text{h}} + E_{\text{L}}\, t_{\text{h}}}{1 + E_{\text{F}}\, t_{\text{h}}} \right), \tag{2.13}$$

which we can rewrite

$$E_{\text{F}}\, v_{\text{F}} + E_{\text{L}}\, v_{\text{L}} > E_{\text{F}}\, v_{\text{F}} \left(1 + \frac{E_{\text{L}}\, t_{\text{h}}}{1 + E_{\text{F}}\, t_{\text{h}}} \right). \tag{2.14}$$

The term $E_{\text{F}} v_{\text{F}}$ now cancels from both sides of the inequality, leaving us

$$E_{\text{L}}\, v_{\text{L}} > \frac{E_{\text{F}}\, v_{\text{F}} E_{\text{L}}\, t_{\text{h}}}{1 + E_{\text{F}}\, t_{\text{h}}}. \tag{2.15}$$

We can now cancel E_{L} from both sides; if we also divide both sides by t_{h} then our condition for optimality of the generalist strategy becomes

$$\frac{v_{\text{L}}}{t_{\text{h}}} > \frac{E_{\text{F}}\, v_{\text{F}}}{1 + E_{\text{F}}\, t_{\text{h}}} \tag{2.16}$$

2.2.5   Conclusions and Predictions

The left hand side of (2.16) represents the rate of energy gain from taking a lean prey item (*i.e.*, the energetic value of the prey, v_{L}, divided by the time required to capture and consume it, t_{h}). The right hand side is equal to the average rate of energy gain of a specialist predator, $W(\text{Specialist})$. We may thus conclude that a predator does best to take lean prey items if and only if the rate of energy gain from any one such item exceeds the average rate of gain that could otherwise be obtained (by specialising on fat prey).

MODEL SUMMARY 2.2 – Prey choice

Model type: discrete optimality model

Strategy set: {Specialist, Generalist}

Currency: long-term average rate of energy gain

Model notation:

E_{F}, rate at which 'fat' prey are encountered

E_{L}, rate at which 'lean' prey are encountered

v_{F}, energetic value of 'fat' prey

v_{L}, energetic value of 'lean' prey

t_{h}, prey handling time

Payoffs:

$$W(\text{Specialist}) = \frac{E_{\mathrm{F}}\, v_{\mathrm{F}}}{1 + E_{\mathrm{F}}\, t_{\mathrm{h}}}$$

$$W(\text{Generalist}) = \frac{E_{\mathrm{F}}\, v_{\mathrm{F}} + E_{\mathrm{L}}\, v_{\mathrm{L}}}{1 + E_{\mathrm{F}}\, t_{\mathrm{h}} + E_{\mathrm{L}}\, t_{\mathrm{h}}}$$

Optimal solutions:

$\dfrac{v_{\mathrm{L}}}{t_{\mathrm{h}}} > \dfrac{E_{\mathrm{F}}\, v_{\mathrm{F}}}{1 + E_{\mathrm{F}}\, t_{\mathrm{h}}}$:　　　　Generalist

$\dfrac{v_{\mathrm{L}}}{t_{\mathrm{h}}} = \dfrac{E_{\mathrm{F}}\, v_{\mathrm{F}}}{1 + E_{\mathrm{F}}\, t_{\mathrm{h}}}$:　Generalist or Specialist

$\dfrac{v_{\mathrm{L}}}{t_{\mathrm{h}}} < \dfrac{E_{\mathrm{F}}\, v_{\mathrm{F}}}{1 + E_{\mathrm{F}}\, t_{\mathrm{h}}}$:　　　　Specialist

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There is an interesting biological implication of the fact that E_{L} (the rate of encountering lean prey) cancelled out in our derivation of condition (2.16) from (2.12). The decision to accept or ignore lean prey items should not depend upon the rate at which they are encountered! Rather, it is the frequency of *fat* items that determines whether the predator should accept lean prey as well (the lower the rate at which fat prey are encountered, the lower the rate of energy intake of a specialist predator, and so the more likely it is to benefit by taking a lean prey item).

2.3   Parental care 2

Our simple, discrete model of parental investment (§2.1) has already told us something about the circumstances that favour parental care. But, as we have hinted, we can learn more by extending the analysis to allow for a larger range of possible strategies. In particular, we would like to allow for variation in the time that a parent devotes to care.

2.3.1   Strategy set

Suppose, then, that a parent must decide not merely whether to care at all, but what duration of time, t, it will devote to its offspring (before leaving to seek a new mate). We will assume that the probability of offspring survival depends on the duration of care — the longer the parent stays, the less likely the offspring are to die. A parent that devotes more time to care will thus raise more surviving offspring per brood. On the other hand, it will not be able to mate as frequently as an individual that immediately abandons its mate and young.

2.3.2   Currency

What is the optimal duration[2] of care, $\hat{t}$, under these circumstances? Once again, to solve the model we must specify our currency (optimisation criterion) and calculate payoffs. In this case, we will choose the rate of offspring production as the most suitable currency (to be precise, the long-term average rate of offspring production). We can then calculate the payoff to a parent that cares for a period t, denoted $W(t)$, as follows.

2.3.3   Payoff

The parent spends its time alternately searching for a mate, and then caring for the offspring of the mating. Let t_s denote the average time spent searching; the total time expended per brood (first finding a mate and then caring for the young) is thus equal to $t_\mathrm{s} + t$.

We can assume a fixed brood size of n, but the proportion of offspring surviving from each brood will depend on the duration of care they receive.

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[2]Throughout this book, we use a 'hat' ˆ to denote an optimal or evolutionarily stable strategy; thus, the optimal duration of care is written $\hat{t}$.

Offspring survival must therefore be specified by a function $s(t)$, which takes the place of the two parameters s_C and s_D in §2.1. Consequently, the long-term average rate of offspring production, $W(t)$ is

$$W(t) = \frac{n\,s(t)}{t_\mathrm{s} + t}\,. \tag{2.17}$$

In the payoff function given in equation (2.17), the caring time t is the quantity on which selection is presumed to be acting (unlike n and t_s, which are presumed to be fixed). We therefore refer to t as an **evolutionary variable**.

2.3.4   Mathematical form of the survival function

To find a precise value for $\hat{t}$, the duration of care that yields the maximum rate of offspring production, we need to specify the shape of the survival function $s(t)$. But this function might take many different forms. How then do we proceed? One option is to try to determine the shape of the function empirically in a suitable study species. Unfortunately, this is likely to prove a lengthy and challenging task.

A simple and reasonable alternative is to investigate the consequences of a particular functional form for $s(t)$. To determine a plausible form for $s(t)$, we must convert biological facts and constraints into mathematical statements about $s(t)$. In our present example, the key properties that we would like $s(t)$ to have are as follows:

- Offspring are bound to die if the parent deserts them immediately, which translates into the mathematical condition

$$s(0) = 0\,. \tag{2.18}$$

- The longer the parent stays, the more likely the young are to survive, *i.e.,* survival probability increases with the amount of time invested in care or, mathematically,

$$s'(t) > 0 \text{ for all times } t\,. \tag{2.19}$$

- Eventually, additional time devoted to care will yield diminishing returns. Thus, there is a time, t_dim, such that

$$s''(t) < 0 \text{ for all times } t > t_\mathrm{dim}\,. \tag{2.20}$$

- Regardless of how much time a parent invests in care, there is a maximum probability of survival of its offspring; moreover, this maximum must be no more than 1, since a probability greater than 1 is nonsense. Since we have assumed that survival is a strictly increasing function of the amount of time invested in care, $s(t)$ must approach its maximum value as t grows larger and larger. Mathematically, this condition is written

$$\lim_{t \to \infty} s(t) = s_{\max} \leq 1 \,. \tag{2.21}$$

In appendix **??**, we discuss how one can find functions that satisfy the above conditions, and how to approach the problem of finding functions that satisfy various other conditions as well. Rather than get sidetracked now on building functional forms, we simply observe that the survival function

$$s(t) = s_{\max} \frac{t}{t + t_{\text{half}}} \,, \tag{2.22}$$

which is illustrated in figure 2.1, has all the required properties (you should check this). The names of the two parameters $s_{\max}$ and t_{half} have been chosen to emphasize their meanings: $s_{\max}$ is the the maximum survival probability, $s_{\max} = \lim_{t \to \infty} s(t)$, and t_{half} is the investment time required to achieve half the maximum survival probability, $s(t_{\text{half}}) = s_{\max}/2$.

2.3.5   Optimal strategy

Remember that the payoff to strategy t, equation (2.17), is the number of surviving offspring per brood, divided by the time expended per brood (on search and care). Given our survival function $s(t)$, the rate of offspring production is

$$W(t) = \frac{n\,s(t)}{(t_{\text{s}} + t)} = \frac{ns_{\max}\,t}{(t_{\text{s}} + t)(t + t_{\text{half}})} \tag{2.23}$$

(we obtain this expression by substituting (2.22) into (2.17)). To find the value of t for which this rate is maximised, we can use some basic calculus. First, we calculate the slope (*i.e.,* derivative) of the payoff function $W(t)$, denoted $W'(t)$. This turns out to be

$$W'(t) = ns_{\max} \frac{t_{\text{half}}\,t_{\text{s}} - t^2}{(t + t_{\text{half}})^2 (t_{\text{s}} + t)^2} \tag{2.24}$$
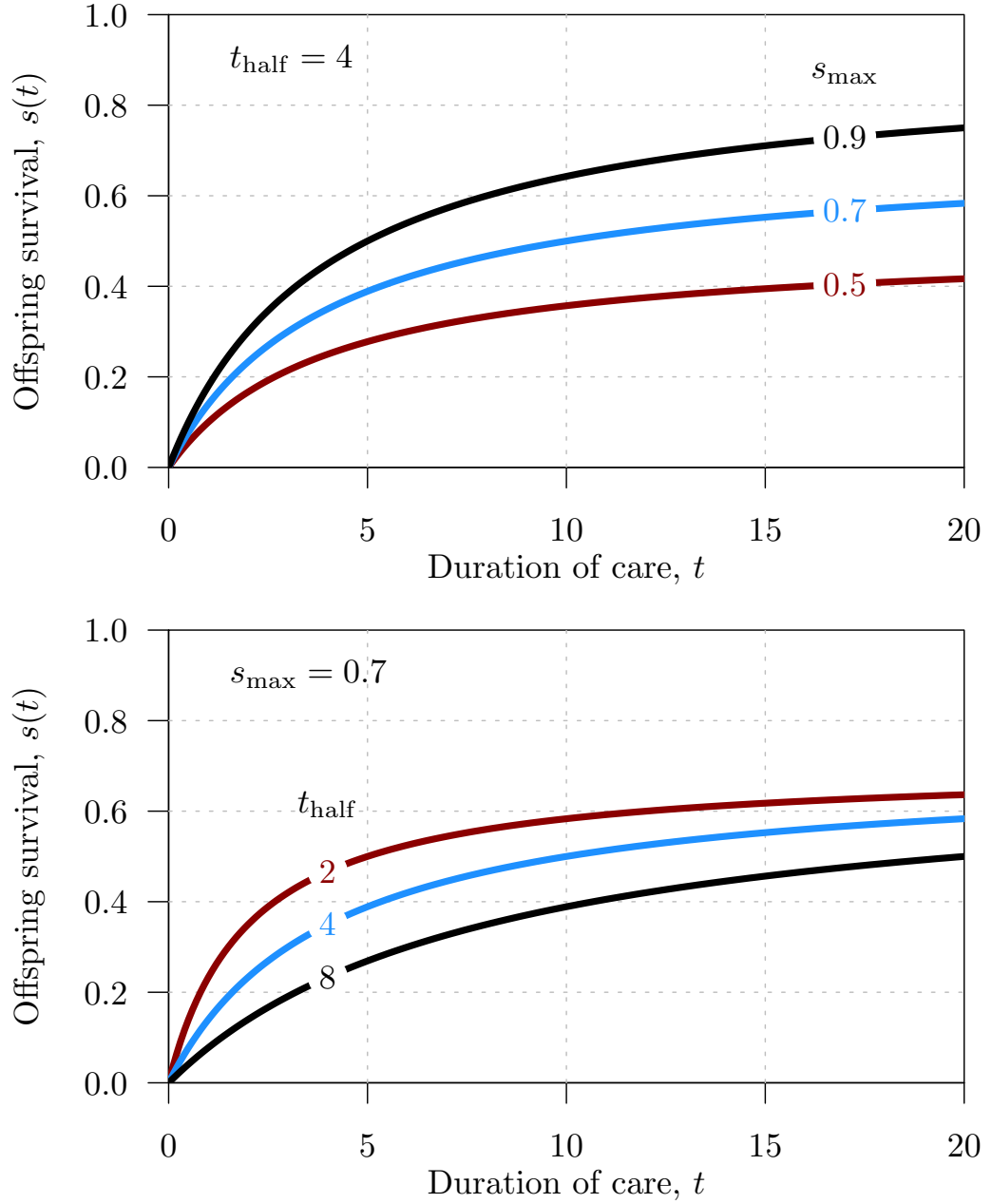
Figure 2.1: The sample survival function given in Equation (2.22). The top panel shows $s(t)$ for three values of $s_{\max}$, 0.5, 0.7 and 0.9, as indicated on the curves, with $t_{\text{half}} = 4$. The bottom panel shows $s(t)$ for three values of t_{half}, 2, 4 and 8, as indicated on the curves, with $s_{\max} = 0.7$.

At a maximum point or minimum point of the payoff function, the slope must equal zero. So the optimal duration of care $\hat{t}$ must satisfy the following equation

$$W'(\hat{t}) = n s_{\max} \frac{t_{\text{half}} t_{\text{s}} - \hat{t}^2}{(t_{\text{half}} + \hat{t})^2 (t_{\text{s}} + \hat{t})^2} = 0 \,. \qquad (2.25)$$

The only possible solution is

$$\hat{t} = \sqrt{t_{\text{half}} t_{\text{s}}} \qquad (2.26)$$

(strictly speaking, $\hat{t} = -\sqrt{t_{\text{half}} t_{\text{s}}}$ represents an alternative solution to equation (2.25), but since a negative duration of care is biologically meaningless, we can ignore this solution).

As a final step, we should confirm that the solution specified by (2.26) represents a maximum point rather than a minimum point of the payoff function, and that it is a global rather than merely a local maximum point. We can check whether it is a maximum point by calculating the second derivative of the payoff function, $W''(t)$. If this is negative when evaluated at $\hat{t}$, then $\hat{t}$ represents a local maximum point (while if the second derivative is positive, $\hat{t}$ represents a local minimum point). In our case, it is easy to confirm that $W''(t)$ is always negative (see exercise 3), so that $\hat{t}$ represents a local maximum. Moreover, since $\hat{t}$ is the only critical point of $W(t)$ for positive caring times, $\hat{t}$ must also be a global maximum point. We can, alternatively, note that $W(t)$ is non-negative for all $t \geq 0$ and zero at $t = 0$ and as $t \to \infty$. Consequently, the unique critical point $\hat{t}$ must be a maximum point, not a minimum point, and we can thus avoid calculating the second derivative of $W(t)$.

To conclude, the optimal duration of parental care, $\hat{t}$ (illustrated in figure 2.2), is the geometric mean of the average search time, t_{s}, and the half-maximum time, t_{half}, of the survival function $s(t)$.

2.3.6   The Marginal Value Theorem

There is an easier way to determine the optimal strategy in our parental care model.

Figure 2.3 presents a simple graphical analysis of the model, with the survival function $s(t)$ given by equation (2.22). Since the number of offspring in each brood (n) is a constant, we can equally well maximize
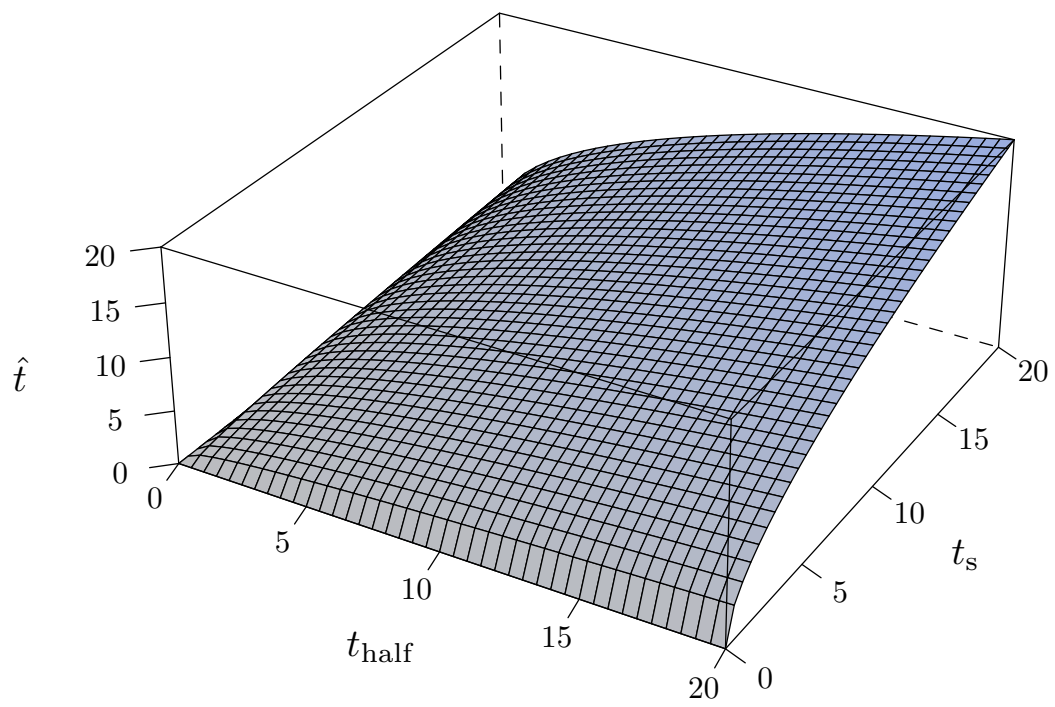
$$\frac{1}{n} W(t) = \frac{s(t)}{t_{\text{s}} + t} \qquad (2.27)$$

Figure 2.2: Optimal duration of care $\hat{t}$ as a function of t_{half} and t_{s}.

Graphically, this quantity is the slope of the line AB in figure 2.3 (since point B lies at height of $s(\hat{t})$ above the x-axis, while the horizontal distance from A to B is equal to $t_{\mathrm{s}} + \hat{t}$). The slope will be maximized if the line is tangent to the survival curve at point B, *i.e.*, if

$$\frac{s(t)}{t_{\mathrm{s}} + t} = s'(t)\,, \tag{2.28}$$

where $s'(t)$ denotes the derivative (*i.e.*, slope) of $s(t)$ at point B. You can see from the lower graph in the figure that either a shorter or a longer duration of care (such as t_1 or t_2) would yield a line AB with a shallower slope and hence would lead to a decrease in the long-term rate of offspring production. Thus, the optimal strategy in our model is the solution of equation (2.28).

The general result that solutions of equation (2.28) yield optimal strategies is known as the **Marginal Value Theorem**. We state this result formally in Theorem 1. The result can be generalized in a useful way, which we discuss in appendix **??**.

Theorem 1 (The Marginal Value Theorem). *Consider a function $s(t)$ with the following properties: $s(0) = 0$, $s'(t) > 0$ for all $t > 0$, and there exists $t_{\mathrm{dim}} \in [0, \infty)$ such that (i) either $t_{\mathrm{dim}} = 0$ or $s''(t) > 0$ for $0 \leq t < t_{\mathrm{dim}}$ and (ii) $s''(t) < 0$ for all $t > t_{\mathrm{dim}}$. If $\alpha > 0$ and*

$$f(t) = \frac{s(t)}{\alpha + t}\,, \qquad t \geq 0\,, \tag{2.29}$$

then $f(t)$ has a unique maximum point $\hat{t} \in (0, \infty)$, which is the solution of the equation $f(\hat{t}) = s'(\hat{t})$.

Proof. Appendix **??**. $\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\square$

In the statement of the Marginal Value Theorem, t_{dim} is the **point of diminishing returns**.

In the context of our current model, the Marginal Value Theorem says that the optimal caring time occurs when the marginal rate of survival equals the long-term average survival rate. If we would like to derive a precise mathematical expression for the optimal duration of care, then the theorem also helps us. All we need to do is solve equation (2.28) for t. There is no need to check anything further.

The graphical analysis can give us a good idea of what to expect from the model, even if we haven't found an explicit formula for the optimal caring
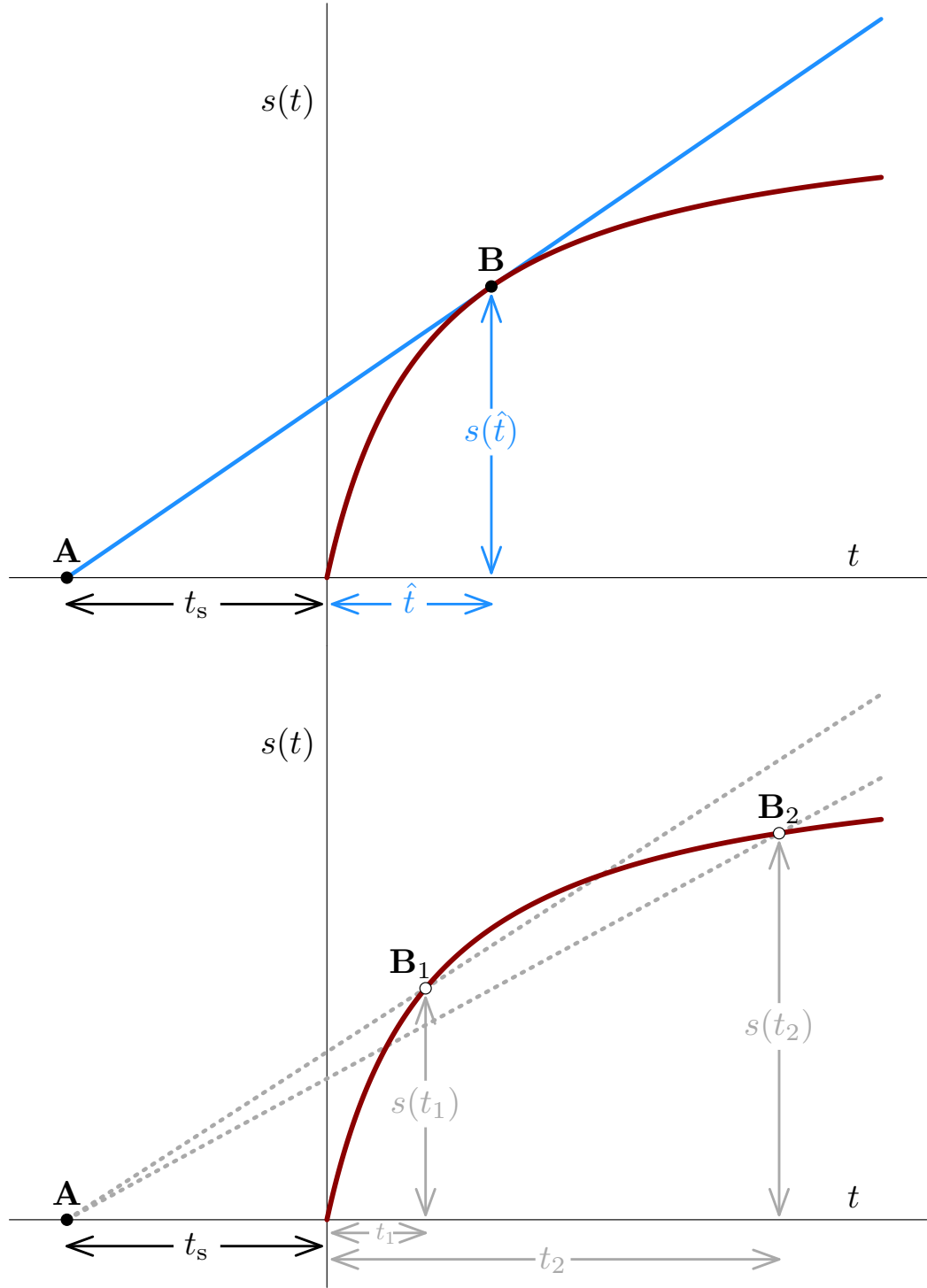
Figure 2.3: Illustration of Marginal Value Theorem (Theorem 1 on page 17). The survival function $s(t)$ in the figure is given by equation (2.22), with $t_{\mathrm{half}} = 4$ and $s_{\max} = 0.9$. The search time is $t_{\mathrm{s}} = 10$. The goal is to maximize the long-term average rate of survival, $s(t)/(t_{\mathrm{s}}+t)$. The top panel illustrates the situation for the optimal care time $\hat{t}$. The bottom panels shows two suboptimal care times, t_1 and t_2.
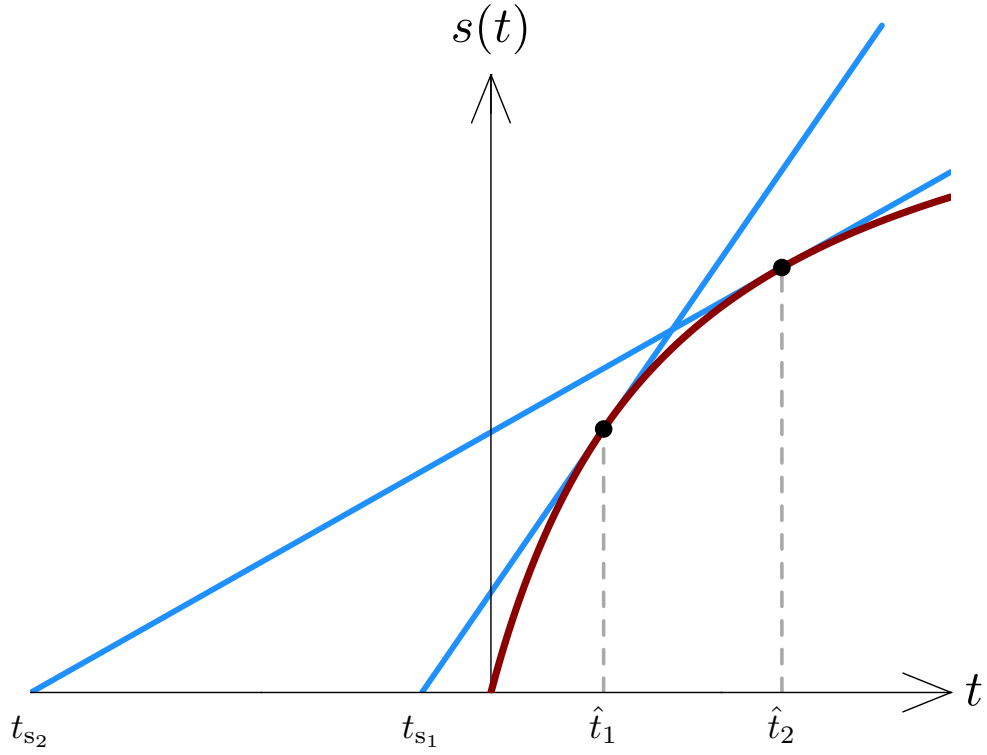
Figure 2.4: Second illustration of Marginal Value Theorem (Theorem 1 on page 17). The survival function $s(t)$ in the figure is given by equation (2.22), with $t_{\text{half}} = 8$ and $s_{\max} = 0.9$. A short search time such as $t_{s_1} = 3$ leads to a short optimal duration of care, $\hat{t}_1$, while a longer search time such as $t_{s_2} = 20$ leads to a longer optimal duration of care, $\hat{t}_2$.

time. For example, it allows us to see immediately how the optimal caring time is affected by reducing or increasing the searching time. As figure 2.4 demonstrates, the optimal duration of care will increase with t_s. The longer it takes to find a new mate, the longer a parent should remain with its young (a result that also holds for other survival functions of similar form).

From a computational point of view, the Marginal Value Theorem (figure 2.3 and equation (2.28)) provides a shortcut to the derivation of the optimal caring time $\hat{t}$. The theorem tells us that the optimal caring time $\hat{t}$ satisfies equation (2.28). Hence, we can solve this equation to find the optimum duration of care. You should try this and check that you get the same value for $\hat{t}$ as we obtained from the "brute force" method in the previous section (see exercise 3).

2.3.7   Conclusions and Predictions

Equation (2.26) gives a precise mathematical representation of our conclusion (obtained graphically from figure 2.3) that the optimal period of care $\hat{t}$ increases with the time required to find a mate. The precise relationship is shown in figure 2.2. $\hat{t}$ also depends on t_{half}, which determines how quickly offspring survival approaches its maximum value (but not on s_{max}, the maximum survival probability itself).

2.3.8   Sensitivity analysis / robustness of predictions

While the explicit solution (2.26) for the dependence of the optimal caring time on t_s and t_{half} is useful, it is not clear how general the result is. For example, if the survival function $s(t)$ has a different mathematical form that nevertheless satisfies all the hypotheses of the Marginal Value Theorem, should we expect the optimal caring time to be proportional to the square root of the search time?

We can gain more insight by repeating our analysis for a number of plausible functional forms for $s(t)$, and looking for predictions common to all (see exercise 3 and problem 5). Such predictions are robust, in the sense that they do not depend on a particular functional form for $s(t)$, only on properties common to all the functional forms we have considered.

The best approach (though much harder) is simply to work with the mathematical properties that we feel the function in question must satisfy

$_{416}$ and derive results depending only on those properties (rather than any par-
$_{417}$ ticular functional form for $s(t)$). This approach is carried through for the
$_{418}$ problem in this section in appendix **??**.

$_{419}$

MODEL SUMMARY 2.3 – Parental care 2

Model type: continuous optimality model

Strategy set: all non-negative values of the duration of care $\{t : t \geq 0\}$

Currency: long-term average rate of offspring production

Model notation:

n, brood size

$s(t)$, survival of current brood as a function of the duration of care

t_{s}, average time spent searching for a new mate

Payoff:

$W(t) = \frac{n\, s(t)}{t_{\mathrm{s}} + t}$

Optimal solution:

Dependent on form of survival function $s(t)$.

For $s(t) = s_{\max} \frac{t}{t + t_{\mathrm{half}}}$, $\hat{t} = \sqrt{t_{\mathrm{half}} t_{\mathrm{s}}}$.

More generally, $\hat{t}$ satisfies $\frac{1}{n} W(\hat{t}) = s'(\hat{t})$ (by Marginal Value Theorem).

$_{420}$ 2.4 Patch exploitation

$_{421}$ In our previous discussion of foraging (§2.2) we considered the optimal for-
$_{422}$ aging strategy of a predator that encounters two prey types (that differ in
$_{423}$ energetic value) at different rates. Suppose instead that a predator encoun-
$_{424}$ ters only one prey type, but that prey are found in isolated patches, between
$_{425}$ which a predator must spend significant time travelling. How long should
$_{426}$ a foraging predator stay in a given patch? The longer it stays, the more
$_{427}$ prey it is likely to obtain. However, the rate of capture is likely to diminish
$_{428}$ with time in a patch, as it becomes depleted. In other words, energetic gain

429 from a patch will be an increasing, but decelerating, function of the time the
430 predator spends there.

2.4.1   Strategy set

432 Our strategy set contains all possible, non-negative choices of t, the patch
433 residence time (*i.e.*, the length of time that a predator stays in any one patch).

2.4.2   Currency

435 As in our previous foraging model, a suitable currency is the long-term av-
436 erage rate of energy gain.

2.4.3   Payoffs

438 To express the long-term average rate of energy gain achieved for each pos-
439 sible strategy t, we need to know

440 - t_{s}, the average time required to search out a new patch, often referred
441   to as the **travel time**.

442 - $g(t)$, a function giving the average energy gain achieved in a patch in
443   which the predator has foraged for time t.

444 The payoff to strategy t is then

$$W(t) = \frac{g(t)}{t_{\mathrm{s}} + t} \tag{2.30}$$

2.4.4   Optimal strategy

447 To determine the optimal strategy, we need to know something about the
448 energy gain function $g(t)$. We are faced with exactly the same problem that
449 we encountered when investigating the optimal caring time in §2.3. As in the
450 parental care model, the optimal patch residence time in our foraging model
451 is determined by the Marginal Value Theorem.   In fact, this is really exactly
452 the same model from a mathematical point of view; the only difference is the
453 interpretation of the parameters and variables.

2.4.5   Conclusions and Predictions

The longer the average search time, the longer the optimal patch residence time. Given a particular functional form for $g(t)$, we can use the Marginal Value Theorem to derive an exact relationship between the optimal residence time t, the average travel time t_s and any parameters that specify the form of $g(t)$.

MODEL SUMMARY 2.4 – Patch exploitation

Model type: continuous optimality model

Strategy set: all non-negative values of patch residence time $\{t : t \geq 0\}$

Currency: long-term average rate of energy gain

Model notation:

> $g(t)$, energy gain from a patch as a function of residence time
>
> t_s, travel time (*i.e.*, average time spent searching for a new patch)

Payoff:

> $W(t) = \frac{g(t)}{t_\mathrm{s}+t}$

Optimal solution:

> Dependent on form of gain function $g(t)$.
>
> In general, $\hat{t}$ satisfies $W(\hat{t}) = g'(\hat{t})$ (by Marginal Value Theorem).

2.5   Size/number tradeoff

The preceding examples may give the impression that the marginal value theorem is always applied to problems involving the maximization of long-term rates. In fact, the theorem applies much more generally.

Consider, for example, a bird that produces a clutch of total mass m_tot, which it divides equally among n eggs (each of mass $m = m_\mathrm{tot}/n$). Egg size is almost certainly related to chick survival, with larger eggs yielding a higher probability of reaching adulthood. If the total clutch mass m_tot cannot be altered, what is the optimal brood size n?

2.5.1   Strategy set

We can take the strategy set to be the set of all possible brood sizes, *i.e.*, the set of natural numbers $\{1, 2, 3, \ldots\}$; equivalently, we can consider the strategy set to be the set of all possible egg masses $\{m_{\mathrm{tot}}, m_{\mathrm{tot}}/2, m_{\mathrm{tot}}/3, \ldots\}$.

2.5.2   Currency

Since we are considering a single reproductive bout, our currency is the number of surviving offspring. This is equivalent to the long-term average rate of offspring production, provided we assume that the time invested in producing and raising a brood is independent of clutch size n.

2.5.3   Payoffs

If we let $s(m)$ denote the probability of survival of an egg of mass m then the payoff to an individual that lays eggs of mass m is

$$W(m) = \frac{m_{\mathrm{tot}}}{m} \cdot s(m) \tag{2.31}$$

2.5.4   Optimal strategy

Since m_{tot} is fixed, maximizing the payoff function $W(m)$ is equivalent to maximizing

$$\frac{s(m)}{m} \tag{2.32}$$

This is the type of function to which the Marginal Value Theorem applies. If you look back at the parental care model in §2.3 or the optimal foraging model in §2.4 you will see that the payoff functions in those cases took a similar form.

We can draw an even closer parallel between the models, if we assume that $s(m) = 0$ for all m less than some minimum viable mass m_{min}. If we define

$$\Delta m = m - m_{\mathrm{min}} \tag{2.33}$$

and

$$\tilde{s}(\Delta m) = s(m_{\mathrm{min}} + \Delta m) \tag{2.34}$$

then

$$\frac{s(m)}{m} = \frac{\tilde{s}(\Delta m)}{m_{\min} + \Delta m}, \tag{2.35}$$

which looks just like our previous analyses involving the marginal value theorem. Here, $m_{\min}$ plays the same role that t_{s} played in the parental care model in §2.3 or the optimal foraging model in §2.4.

Making use of the Marginal Value Theorem, we know that the maximum payoff occurs at the value of m such that[3]

$$\frac{\tilde{s}(\Delta m)}{m_{\min} + \Delta m} = \tilde{s}'(\Delta m) \tag{2.36}$$

or, equivalently[4],

$$\frac{s(m)}{m} = s'(m). \tag{2.37}$$

The form of the survival function $s(m)$ will be similar to the survival function $s(t)$ considered in §2.3: eggs that are too small won't survive, but increasing egg size eventually yields a positive payoff, with diminishing returns for increased investment per offspring.

---

[3]Strictly speaking, the function $s(m)/m$ is defined only at discrete values of $m \in \{m_{\mathrm{tot}}, m_{\mathrm{tot}}/2, m_{\mathrm{tot}}/3, \ldots\}$. If we treat m as a continuous variable then the Marginal Value Theorem does apply, but it may yield an optimal egg size that is not in the strategy set. If $\tilde{m}$ is the optimal egg size identified by the Marginal Value Theorem then the optimal strategy $\hat{m}$ will be one of the two accessible egg sizes nearest to $\tilde{m}$. Both these egg sizes must be checked to determine the optimum.

[4]Note that $\tilde{s}'(\Delta m) = \frac{d[s(m_{\min} + \Delta m)]}{d[\Delta m]} = \frac{d[s(m)]}{dm} \times \frac{\partial m}{\partial[\Delta m]} = s'(m)$.

MODEL SUMMARY 2.5 – Offspring size/number tradeoff

Model type: discrete optimality model

Strategy set: all non-negative values of egg mass $m \in \{m_{\text{tot}}, m_{\text{tot}}/2, \ldots\}$

Currency: expected reproductive success

Model notation:

m_{tot}, total clutch mass

$s(m)$, offspring survival as a function of egg mass

Payoff:

$W(m) = m_{\text{tot}}.\frac{s(m)}{m}$

Optimal solution:

Dependent on form of survival function $s(m)$.

In general, $\hat{m} \approx \tilde{m}$, which satisfies $\frac{1}{m_{\text{tot}}}W(\tilde{m}) = s'(\tilde{m})$ (by Marginal Value Theorem).

2.5.5   Conclusions and Predictions

The mathematical form of the present model is identical to the parental care model in §2.3, but the implications of the results are different in each case. Here we are considering optimal allocation within a given brood, rather than the tradeoff between investment in the current brood and investment in subsequent broods. We predict that the optimal size of an individual egg increases with the minimum size required for viability. Optimal egg size is, however, independent of total clutch mass. In other words, parents with more to invest should produce *more* young rather than *larger* young.

2.6   Summary

In formulating an optimality model, you must specify:

- The strategy set (which may be discrete or continuous).

- The currency (*i.e.,* the optimisation criterion).

- The model parameters.

- The payoffs to the various possible strategies.

To fully solve the model, you must determine (for all plausible parameter values) which strategy or strategies yield the greatest payoff.

2.7   Notes and Further Reading

To be added...

Exercises 2

1. In the discrete parental care model summarized on page 7, suppose that offspring of a parent who cares are twice as likely to survive as those of a parent who deserts and three times as likely to survive as offspring in a second brood. Suppose also that a parent who deserts succeeds in remating 50% of the time. What parental behaviour is favoured by natural selection?

   Solution to this problem.

2. Consider a predator that encounters two types of prey while foraging. 'Smooth' prey require a handling time t_{hs}, while 'prickly' prey require a handling time t_{hp} ($> t_{hs}$). Both types of prey have the same energetic value and are encountered at the same rate E. Consider two alternative foraging strategies: 'specialists' will attack only smooth prey (and will ignore prickly items), whereas 'generalists' will take both prey types. The currency, which acts as a proxy for fitness in this context, is the long-term average rate of energy intake. Write down the payoffs to the specialist and generalist strategies and show that natural selection will favour the generalist strategy if and only if $t_{hp} < t_{hs} + (1/E)$. Does this result make sense?

3. For the second parental care model summarised on page 21, with $s(t)$ as specified by equation (2.22), show that

(a) $W(t)$ does indeed have its maximum value at $t = \hat{t}$, defined in equation (2.26). *Hint:* See §2.3.5 for discussion of how this might be done.

(b) The solution to equation (2.28) (*i.e.,* the solution given by the Marginal Value Theorem) matches the solution given in (2.26).

Use the Marginal Value Theorem to obtain the optimal duration of parental care $\hat{t}$ for each of the following alternative survival functions (you may assume that each survival function satisfies the properties outlined in the Marginal Value Theorem).

(c) $s(t) = \frac{t^2}{(1+t)^2}$.

(d) $s(t) = \sqrt{\frac{t}{1+t}}$.

(e) $s(t) = a \left(\frac{t}{1+(t/b)} \right)^c$, where a, b and c are positive constants.

4. In the offspring size/number tradeoff (page 26), suppose that in a clutch of N eggs, each offspring survives with probability $1/(1 + N)$. What clutch size is favoured by natural selection? Does the answer depend on the total clutch mass?

Problems 2

1. *Mouthbrooding fish.* Fish of a certain species breed at most twice each summer. Each reproductive bout consists of the following steps:

- The female lays a clutch of eggs (always the same number of eggs).

- The male fertilizes the eggs.

- Both parents pick up the eggs in their mouths (*each parent takes half the clutch*).

In order to survive, eggs must be protected in a parent's mouth for several weeks. Males always provide this parental care, but females have a choice:

- Females can *care* for their first clutch, in which case they cannot remate a second time (because they do not have time to build up

sufficient resources to produce a second clutch of eggs in the same breeding season).

- Females can eat (*i.e.*, *cannibalize*) the fertilized eggs they have picked up. In this case, this extra food replenishes their resources sufficiently to allow them to produce and care for a second clutch. The catch is that cannibalistic females will find a second mate only with some (known) probability less than 1.

Under what circumstances will natural selection favour females that cannibalize their first clutch? Support your answer with an optimality model. Clearly identify the strategy set, an appropriate currency, and derive expressions for the payoffs to each strategy. Derive a formal condition for optimality of the 'cannibal' strategy and comment on the biological meaning and plausibility of your result.

2. *Foraging.* A predator encounters two types of prey while foraging. Fat prey of energetic value v_{F} are encountered at rate E_{F}, while lean prey (of value $v_{\mathrm{L}} < v_{\mathrm{F}}$) are encountered at rate E_{L}. Unlike the the prey choice example on page 10, suppose that the time needed for capture and consumption is different for the two types of prey. Fat prey require a handling time t_{hF} while lean prey require a handling time t_{hL}.

Predators can take only fat prey ('F-specialist' strategy) only lean prey ('L-specialist' strategy) or whatever they come across ('generalist' strategy). Under what circumstances will natural selection favour generalist predators? Support your answer with an optimality model. Clearly identify and explain the strategy set, the currency, and derive expressions for the payoffs to each strategy. Derive a formal condition for optimality of the 'generalist' strategy and comment on the biological meaning and plausibility of your result.

3. *Patchy foraging.* For a certain predator, the average travel time between suitable foraging sites (habitat patches) is one minute. The energy gained from foraging in a patch for t minutes is proportional to $\ln\left(1 + t\right)$. How long should the predator stay in each patch before moving on? Support your answer with an optimality model. Clearly specify the strategy set, the currency and the payoff to each strategy. Determine the optimal strategy using the Marginal Value Theorem.

4. *Seductive dung.* Dung flies of the species *Scatophaga mathematicus* breed continuously and behave as follows. A male searches for a fresh pile of dung (this takes four minutes on average); he then stakes out this fragrant territory until he attracts a female (which takes three minutes on average). When a female arrives, she accepts sperm from the male and stores it in her reproductive tract (this takes two minutes on average). She then lays 100 eggs (at a constant rate of one egg per minute) into the dung; eggs are fertilized as they pass through her reproductive tract and a fixed proportion always survive. If the male guards the female until all 100 eggs have been laid then all her offspring will be his. If he guards for a time t less than 100 minutes then he will be the father of only a proportion $p(t)$ of the female's total offspring, where

$$p(t) = \left(\frac{101}{100}\right)\frac{t}{t+1} \tag{2.38}$$

(the rest of the female's offspring will be fathered by other males, who mate with her before she has finished laying her 100 eggs). Of course, a male can remate sooner if he abandons a female before she has laid her full clutch of eggs.

How long should a male dung fly guard each of his mates? *i.e.,* what guarding time is favoured by natural selection? Support your answer with an optimality model. Clearly identify and explain the strategy set, an appropriate currency, any parameters in your model, and derive an expression for the payoff to each strategy. Find the strategy that yields the maximum payoff (carefully justifying any claims you make) and comment on the biological meaning and plausibility of your result.

Hint: You will probably find the solution more quickly if you make use of the Marginal Value Theorem (to apply the theorem, be sure to check that $p(t)$ satisfies all conditions).

5. *The Marginal Value Theorem.* Reconsider the continuous strategy set parental care optimality model (summarized on page 21).

   (a) Suppose the survival function is given by

$$s(t) = s_{\max}\frac{(t/t_*)^2}{1 + (t/t_*)^2}\,. \tag{2.39}$$

Plot this function and show that the Marginal Value Theorem applies in this case. To do this you must show that $s(0) = 0$, $s'(t) > 0$ for all $t > 0$, and you must show that there is a time t_{dim} such that (i) either $t_{\text{dim}} = 0$ or $s''(t) > 0$ for $0 \leq t < t_{\text{dim}}$ and (ii) $s''(t) < 0$ for all $t > t_{\text{dim}}$. If possible, express t_{dim} as a function of the parameter t_*. What is the meaning of the parameter t_*? Show that the maximum possible value of $s(t)$ is s_{max} by evaluating $\lim_{t \to \infty} s(t)$. Then, use the Marginal Value Theorem to derive a cubic equation for the optimal caring time $\hat{t}$, and explain why this equation shows that $\hat{t}$ is a function of t_* and t_{s} but not s_{max}. Is there a biological explanation for the fact that $\hat{t}$ does not depend on s_{max}? Find an explicit formula for $\hat{t}$ in the special cases $t_{\text{s}} = 0$ and $t_{\text{s}} = \sqrt{3}\, t_*$. (It is possible to find a general explicit formula for $\hat{t}$ for any t_{s} and t_*, but the result is quite messy.)

(b) Plot the survival function

$$s(t) = s_{\text{max}}(1 - e^{-t/t_*}), \tag{2.40}$$

and repeat part (a) with this function. In this case the equation for $\hat{t}$ is not cubic and you (probably) can't solve it. Why is it still possible to conclude that $\hat{t}$ has a unique solution?

(c) Experiments on a certain organism indicate that the survival function is exactly that given in part (b); moreover, the duration of parental care observed in nature (over hundreds of generations of the study organism) is always found to be t_*. Can you predict the average time it takes for an individual to find a mate (as a function of t_*)? Explain your reasoning.

(d) Given the various different survival functions that you have now analyzed (including the one discussed in the main text of this chapter and in the exercises) comment on the significance of the form of the survival function for the evolutionary outcome expected. Put another way, how does the functional form of the survival function influence predictions concerning the strategy to which evolution by natural selection is likely to converge? In particular, how would predictions change if the survival function did not satisfy the hypotheses of the Marginal Value Theorem, and can you think of a functional form that doesn't satisfy those hypotheses but is still biologically plausible?

Projects 2

1. *Brood parasites.* Cuckoos do not care for their young. However, cuckoo chicks cannot survive without parental care (in particular, they must be fed). Parent cuckoos arrange for care of their young by tricking birds of another species. Typically, a female cuckoo removes an egg from the nest of a bird of another species (called the 'host' species) and lays an egg of her own to replace it. This is all done very quickly at a time when the host parent is away foraging. If the host does not remove the cuckoo egg before it hatches, then the cuckoo chick (which always hatches first) will destroy all the other eggs in the nest. The host then feeds the cuckoo chick until it fledges (*i.e.,* until it can fly away and take care of itself); from an evolutionary perspective the host thus wastes all its parental effort, since it fails to raise any offspring of its own.

   (a) A warbler suspects that one of the n eggs in its nest is a cuckoo egg. There is a certain probability that the egg in question really is a cuckoo egg. The warbler has two options, either to accept the suspicious egg or to eject it from its nest and care for the remaining $n - 1$ eggs. Under what circumstances will natural selection favour acceptance of the suspicious egg? Support your answer with an optimality model. Clearly identify and explain the strategy set, the currency, any parameters in the model, and derive expressions for the payoffs to each strategy. Derive formal conditions for optimality of the 'accept' and 'eject' strategies and comment on the biological meaning and plausibility of your result.

   (b) Suppose the warbler is certain that it has been parasitized by a cuckoo (*e.g.,* because it has witnessed a cuckoo laying an egg in its nest) but that it cannot identify which of the eggs in its nest is the cuckoo egg. What should the warbler do? *i.e.,* what behavioural response will be favoured by natural selection? *Hint:* options available to the warbler might include accepting the cuckoo egg or ejecting one or more eggs from the nest.

2. *Mate choice.*

   In our analysis of parental care, we envisoned an individual alternating between searching for a mate and caring for the offspring of the mating.

Let us shift our focus now to the former activity.

Animals do not always accept the first potential partner they encounter when searching for a mate. Rather, in some species, they will actively reject one mate in favour of another. To give an extreme example, a peahen may approach up to a dozen peacocks when searching for a mate. This kind of choice is thought to reflect the fact that some mates are 'better' than others — superior partners may offer a substantial courtship gift, or a safe or well-provisioned territory; they may prove better parents, or even perhaps produce offspring that survive better or grow up to become more attractive adults.

Consider a peahen who is searching for a mate. We will assume that she encounters new potential partners one-at-a-time, and must decide whether to accept and mate with each. If she rejects a male, she cannot subsequently return to him; rather, she simply continues to sample new partners. Males vary in their value to the peahen as mates.

3. *Friend or foe?*

Consider a paper wasp standing guard at the entrance to the colony. Another individual approaches — it might be a closely related nest-mate, or an unrelated intruder. The sentry always does best to admit a nestmate, but to repel an intruder (we assume there is a fitness cost associate with responding inappropriately in either case). But how can she distinguish between the two?

We know that wasps are sometimes able to identify nestmates on the basis of chemical cues. These may be genetically encoded, or may be absorbed from plant fibres in the nest itself. But these cues do not provide a perfect means of identification. In practice, nestmates and strangers are likely to exhibit overlapping sets of cues. A sentry thus cannot avoid the possibility of error.

Two different kinds of error are possible. The sentry may mistakenly reject a nestmate, or mistakenly accept an intruder. We will refer to these as rejection errors and acceptance errors. Inevitably, there is a trade-off between the two. By exercising extreme caution, a sentry may reduce the probability of an acceptance error. But in doing so, she is likely to increase the risk of mistakenly rejecting a nestmate. Conversely, a more tolerant sentry can reduce the risk of rejection errors.

754   But in doing so, she is likely to increase the risk of allowing a stranger
755   to enter the nest.

756   What is the optimal balance between acceptance and rejection errors?
757   To address this question, develop a simple optimality model of discrim-
758   ination, using the following notation.

759   Consider a sentry who must choose whether to accept or reject an
760   approaching individual. With probability p the latter is a nestmate,
761   with probability $1 - p$ an intruder. Four outcomes are possible: correct
762   acceptance of a nestmate, correct rejection of an intruder, mistaken
763   rejection of a nestmate, and mistaken acceptance of an intruder. Let's
764   call the fitness payoffs to the sentry of these outcomes w_{ca}, w_{cr}, w_{mr} and
765   w_{ma}, respectively. Since it is better to accept than to reject a nestmate,
766   and better to reject than to accept an intruder, we can assume that
767    $w_{\mathrm{ca}} > w_{\mathrm{mr}}$ and that $w_{\mathrm{cr}} > w_{\mathrm{ma}}$.

768   The sentry can compare the chemical cues presented by an approach-
769   ing individual with the odour typical of her nestmates, and assess the
770   mismatch between the two. The degree of dissimilarity will typically
771   be less for a nestmate than for a stranger, but not always. Formally,
772   let x denote the degree of dissimilarity. For a nestmate, x is randomly
773   distributed with probability density function $F_n(x)$. For a stranger,
774   the corresponding density function is $F_s(x)$. We will assume that these
775   distributions are of the form shown in figure **??**. In other words, while
776   average dissimilarity is lower for nestmates than for strangers, the two
777   distributions overlap.

778   It is clear that the sentry should reject individuals whose cues are suf-
779   ficiently dissimilar to the odour typical of nestmates (as they are more
780   likely to be strangers). But where, exactly, should she draw the line?
781   Formally, we assume that the sentry will reject an individual whose dis-
782   similarity from the typical odour of the nest exceeds a critical threshold
783   t. We then seek to determine the optimal value of t. A low threshold
784   means that even a slight degree of dissimilarity will trigger rejection.
785   This minimises acceptance errors, but leads to a high risk of rejection
786   errors. Conversely, a high threshold implies that the sentry will tolerate
787   substantial dissimilarity. This minimises rejection errors, but leads to
788   a high risk of acceptance errors.

789   The payoff to a sentry that adopts a rejection threshold of t, which we

denote $W(t)$, is

$$W(t) = p\left[\int_{x<t} w_{\text{ca}}F_n(t)\,dx + \int_{x>t} w_{\text{mr}}F_n(t)\,dx\right]$$
$$+ (1-p)\left[\int_{x<t} w_{\text{ma}}F_s(t)\,dx + \int_{x>t} w_{\text{cr}}F_s(t)\,dx\right] \quad (2.41)$$

The optimal value of t must satisfy

$$W'(t) = 0 \tag{2.42}$$

We therefore differentiate (2.41) to obtain

$$W'(t) = pF_n(t)(w_{\text{ca}} - w_{\text{mr}}) - (1-p)F_s(t)(w_{\text{cr}} - w_{\text{ma}}) \tag{2.43}$$

We can then solve for which $W'(t) = 0$, yielding

$$\frac{F_s(t)}{F_n(t)} = \frac{p(w_{\text{ca}} - w_{\text{mr}})}{(1-p)(w_{\text{cr}} - w_{\text{ma}})} \tag{2.44}$$

The optimal value of t must satisfy equation (2.44).

To determine precisely this optimal value, we must specify the precise form of the distributions $F_n(d)$ and $F_s(d)$. Let's assume that both are normal distributions, with variance σ^2 and mean μ_n and $\mu_s (> \mu_n)$, respectively. Thus

$$F_n(t) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[\frac{(t - \mu_n)^2}{2\sigma^2}\right] \tag{2.45}$$

$$F_s(t) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left[\frac{(t - \mu_s)^2}{2\sigma^2}\right] \tag{2.46}$$

It then follows that

$$\frac{F_s(t)}{F_n(t)} = \exp\left[\frac{(\mu_s - \mu_n)(2t - (\mu_s + \mu_n))}{2\sigma^2}\right] \tag{2.47}$$

If we substitute (2.47) into (2.44) we find that

$$\exp\left[\frac{(\mu_s - \mu_n)(2t - (\mu_s + \mu_n))}{2\sigma^2}\right] = \frac{p(w_{\text{ca}} - w_{\text{mr}})}{(1-p)(w_{\text{cr}} - w_{\text{ma}})} \tag{2.48}$$

We can then solve for t

$$t = \tag{2.49}$$

Bibliography

[1] Maynard Smith J. Evolution and the Theory of Games. Cambridge, UK: Cambridge University Press; 1982.