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canonical equations of SDLHT.

- A section on the Euler-Lotka equation, which underlies both demography and population biology. Although there are underlying mathematical complexities, we can easily derive the Euler-Lotka equation given a schedule of survival and reproduction. (Solution is a bit more complicated, so I discuss the solution by Newton's method in an Appendix.)
- Unpacking the schedule of survival and reproduction, in which we (you, the reader, and I) explore how to link environment and physiology via natural selection to predict the schedules of survival and reproduction. I explain the logic underlying Stochastic Dynamic Programming (which has a rich mathematical history) and derive the two canonical equations for SDLHT. In the first canonical equation, fitness is assessed at the end of a non-breeding period during which the focal organism can choose from among a suite of activities. In the second canonical equation, fitness is accrued over the course of the organism's life.
- Ways of constructing probability distributions for predicted behaviors by allowing errors in decision proportional to the difference in fitness between the optimal decision and an alternative decision.
- Forward Monte Carlo simulation that allows us to predict behavioral or life history observations on the basis of the results of the SDP backward iteration.
- Numerical solution of the canonical equations, including code provided for both canonical equations (Appendices B and C).
- Illustration of how the canonical equations change with bioenergetically based growth models, with considerable attention to the von Bertalanffy growth model and Ray Beverton's use of it in his theory of Growth, Maturity, and Longevity (GML), and lesser attention to the Kleiber-Brody growth model.
- Appendices on the solution of the Euler-Lotka equation (Appendix A), codes for the canonical equations (Appendices B, C), and linear interpolation for non-integer values of the state variables (Appendix D).

52 Introduction

53 Evolutionary ecology should show us both how ecological factors shape fitness and how
54 evolution by natural selection changes ecological interactions (Bassar et al 2012) and
55 SDLHT has become one of the most important tools for generating quantitative predic-
56 tions in evolutionary ecology. These models link organism physiology and environment in
57 a consistent Darwinian framework, allowing us to focus on relevant tradeoffs. For exam-
58 ple, for a foraging animal in a non-reproductive season the tradeoff is between starvation
59 risk and predation risk. During times of reproduction, the tradeoff is between increasing
60 reproduction now, at the possible costs of density-dependent competition among offspring
61 and/or less reproduction in the future, or between current reproduction and survival to
62 a future reproductive opportunity.

63 Organisms use many different strategies to deal with potential starvation-predation
64 (McCue 2011, Scharf 2016) or reproduction-survival tradeoffs (Stone et al 2011). Often
65 these tradeoffs are easy to see (e.g., van der Meijden et al 1988, Negreiros et al 2016, Tietze
66 and Gerald 2016). Sometimes these tradeoffs are hard to see. For example, a salmonid
67 that matures in freshwater is almost always among the fastest growing of its cohort. One
68 might ask: where is the cost of reproduction when the maturing individuals are the fastest
69 growing? But we do not know how much more that individual would have grown had
70 it not matured. Other times, behavior itself might be a tradeoff, simultaneously driving
71 and slowing evolution by natural selection (Munoz and Losos (2018)). Indeed, plasticity
72 in behavior may mean that the ‘wrong’ rules will persist in populations much longer than
73 if behavior were fixed.

74 We assume that SDLHT has a genetic basis, but it will usually be in the background.
75 One reason is that it is likely that there are many more genetic ways to solve the problem
76 of successful reproduction than there are phenotypic ways. That is, for a given environ-
77 ment, phenotype frequency distributions are more predictable than gene frequencies. The
78 conservation of phenotypic traits among these genetically different populations is due to
79 the multi-layered trait architecture, in which one adaptation at a higher architectural
80 level can be achieved by several different adaptations at a lower level (Figure 1). This
81 is an example of convergent evolution (e.g. Moore and Willmer 1997, Conway Morris
82 2009, McGhee 2011, Losos 2011, 2017, Orgogozo 2015, Vermeij 2006). Colleagues at the
83 University of Bergen and I investigated how multi-layered trait architecture and its as-
84 sociated constraints prescribe diversity. Using an idealized model of the emotion system

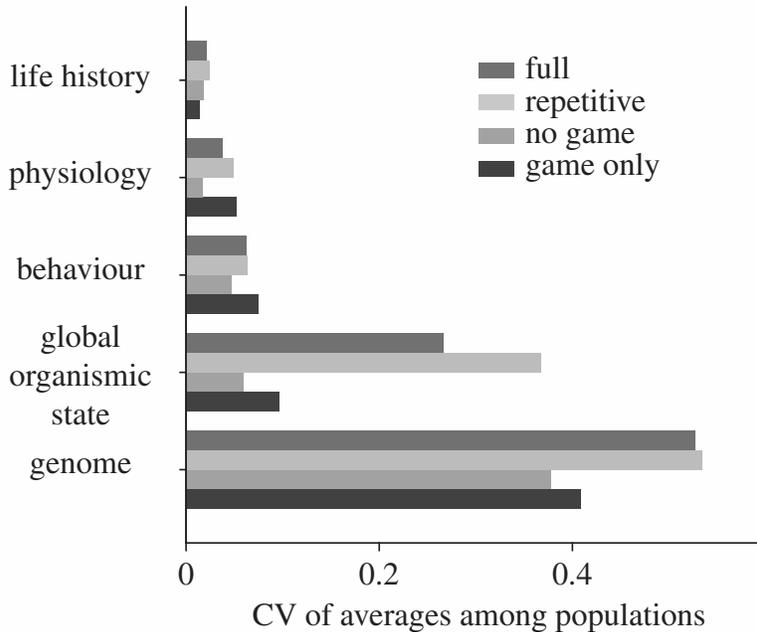


Figure 1: Genotypic and phenotypic diversity, measured by the Coefficient of Variation (CV), within and between scenarios for a model of the emotion system in fish (Giske et al 2014). The four bars represent alternative modeling scenarios that are explained in the paper. Note the shrinkage in CV as the level of biological organization becomes more macroscopic. Comparing the CVs life history and genome we conclude that there are many more ways to solve the problem of successful reproduction at the genomic level than there are at the life history level.

85 in fish, we found that trait architecture yields genetic and phenotypic diversity even in
 86 absence of frequency-dependent selection or environmental variation (Giske et al 2013,
 87 2014, Andersen et al 2016, Eliassen et al 2016).

88 McNamara (1993) identified six questions that life history theory can answer: 1) What
 89 is the intrinsic rate of increase of a population following a given strategy and how does
 90 one find it? 2) What is the expected future reproduction of an organism at its current
 91 age, and how does one calculate it? 3) How does one decompose reproductive value into
 92 current and future reproductive success? 4) How do we predict the effort an organism puts
 93 into current reproduction at the expense of future reproduction? 5) How does individual
 94 behavior link to population growth rates? 6) What mathematical quantity should an
 95 organism maximize over its lifetime?

96 These will always be good questions, although I would replace ‘should an organism
 97 maximize’ with ‘do we predict an organism maximizes’ because ‘should’ is loaded with
 98 context which suggests that deviation from prediction and observation means that the

99 entire predictive edifice is wrong when in fact deviation from prediction and observation
100 means that we have more to explain.

101 To answer the questions, we begin with the Euler-Lotka equation of population demog-
102 raphy. The Euler-Lotka equation presupposes a schedule of survival and reproduction;
103 based on these we compute the growth rate of a population with this schedule, assuming
104 that density dependent interactions can be ignored. If we envision that the schedule of
105 survival and reproduction is linked to a genotype, then the solution of the Euler-Lotka
106 equation is the rate of growth of that genotype, absent density dependence, mutation or
107 other competing genotypes. After analyzing the Euler-Lotka equation, we are lead most
108 naturally to ask “Where do those schedules of survival and reproduction come from?”,
109 with the answer that they involve the interaction of physiology, environment, and behavior
110 via natural selection. To characterize that interaction, we turn to SDLHT.

111 In this chapter we will explore the canonical equations of SDLHT. According to my
112 *Webster’s New World Dictionary, Third College Edition* one definition of canon as “an
113 established or basic rule or principle”. The canonical equations (Mangel 2015) are the
114 foundations on which specific applications can be built. Indeed, one reason to do theory,
115 which is well illustrated by the canonical equations, is that things that appear to be wildly
116 different on the surface are exactly the same in principle. By tailoring the canonical
117 equations to the situation of interest (which is as much art as science) we are able to
118 bring insight from these equations into specific problems in biology.

119 **The Euler Lotka Equation**

We imagine a population of identical individuals growing in the absence of density de-
pendent effects and follow the survival and reproduction of individuals as a function of
age, specifying the survival $l(a)$ of individuals from birth to age a , reproduction $b(a)$ at
age a . If A denotes an effective maximum age (e.g. maximum age span or reproductive
senescence) the first metric for the dynamics of the population is the lifetime reproduc-
tive output of an individual, usually denoted by R_0 , which is obtained by summing the
product of survival to age and reproduction at age

$$R_0 = \sum_{a=0}^A l(a)b(a) \tag{1}$$

120 If $R_0 < 1$ individuals are not replacing themselves and the population will decline over
 121 time; if $R_0 = 1$ individuals are exactly replacing themselves so the population will remain
 122 stable; if $R_0 > 1$ each individual produces more than one offspring over the course of its
 123 life so that the population will grow in time.

To calculate the rate of growth of the population, given the schedule of survival and reproduction, imagine this situation: an uninhabited region is invaded by an individuals of a species with the schedule of survival and reproduction $\{l(a), b(a)\}$. After a while the population will settle down into a regular pattern of survival and reproduction. The offspring born at this time, $B(t)$ are produced by mothers who were born at time $t - a$ and who survived until this time. Since these mothers can be of any age, we obtain the balance equation linking current and previous births

$$B(t) = \sum_{a=0}^A B(t-a)l(a)b(a) \quad (2)$$

124 This equation tells us how the population renews itself.

125 To solve Eqn 2, recall from elementary population dynamics that without density
 126 dependent factors, a population will grow exponentially in time¹, so let us guess that
 127 the solution to Eqn 2 is of the form $B(t) = Ce^{rt}$ where C and r are constants to be
 128 determined.

Putting this guess into Eqn 2, we obtain

$$Ce^{rt} = \sum_{a=0}^A Ce^{r(t-a)}l(a)b(a) \quad (3)$$

which we can rewrite as

$$Ce^{rt} = Ce^{rt} \sum_{a=0}^A e^{-ra}l(a)b(a) \quad (4)$$

and note that C divides from both sides. This means that we will be able to obtain the rate of growth r but not the size of the population from this equation unless we are given ancillary information. Dividing both sides of Eqn 4 by e^{rt} we obtain

$$1 = \sum_{a=0}^A e^{-ra}l(a)b(a) \quad (5)$$

¹That is, in discrete time population numbers follow $N(t+1) = \lambda N(t)$ so that $N(t) = \lambda^t N(0) = \exp[\log(\lambda)t]N(0)$ and in continuous time $\frac{dN}{dt} = rN$ so that $N(t) = e^{rt}N(0)$.

129 which is called the Euler-Lotka equation. Eqn 5 is an equation for the growth rate r of
 130 the population, given the schedule of survival and reproduction. The question remains
 131 how we solve this equation, and since it is a little bit of a detour from our main direction,
 132 I have put it in Appendix A.

R. A. Fisher introduced the concept of reproductive value, which is a measure of future reproduction not from birth, but from some later age a . This can only make sense if the organism is alive at age a , so we introduce the probability $l(a'|a)$ that the individual is alive at a time $a' > a$ given that it is alive at age a^2 . In analogy to Eqn 1, the accumulated reproduction from age a onwards is

$$R_a = \sum_{a'=a}^A l(a'|a)b(a') \quad (6)$$

Since $l(a|a) = 1$ (the probability that the individual is alive at age a given that it is alive at age a must be 1), we can decompose the right hand side of Eqn 6 into current reproduction (i.e. at age a) and all future reproduction, as in

$$R_a = b(a) + \sum_{a'=a+1}^A l(a'|a)b(a') \quad (7)$$

133 This equation takes us to one of the starting points of SDLHT – the balance between
 134 current and future reproduction.

We can do the same kind of calculation with the Euler-Lotka equation, which is how Fisher defined reproductive value at age a , denoted by V_a , and which can be interpreted as the present value of all future reproduction from age a onwards given that the population is growing at rate r

$$V_a = \sum_{a'=a}^A e^{-r(a'-a)}l(a'|a)b(a') \quad (8)$$

135 Clearly V_a can be decomposed into reproduction at age a and reproduction after that, as
 136 we did above (try it yourself!).

²I am assume that you have a working knowledge of basic probability, as reviewed in my previous books [Mangel and Clark (1988), Hilborn and Mangel (1997), Mangel (2006)]. For example, from the definition of conditional probability $l(a'|a) = \frac{l(a')}{l(a)}$.

137 **Unpacking the Schedule of Survival and Reproduction: Link-**
138 **ing Environment, Physiology, and Natural Selection through the**
139 **Canonical Equations of State Dependent Life History Theory**

140 The Euler-Lotka equation tells us a lot, once we are given the schedule of survival and
141 reproduction. However, how are these schedules determined in a more fundamental,
142 mechanistic way? Hypothetically, what would be the “best” schedule of survival and
143 reproduction – that is, the one that makes R_0 or r as large as possible. The simple answer
144 is the Darwinian demon: an organism born ready to reproduce, that never senesces, and
145 lives forever. Darwinian demons do not exist (or at least have not been discovered) because
146 of tradeoffs and constraints. In other words, the schedule of survival and reproduction
147 is an emergent property of the interaction between the physiology of the organism and
148 the biotic and abiotic environment; our challenge is to understand how that interaction is
149 mediated by natural selection into the emerging schedules of survival and reproduction. In
150 order to obtain schedules that account for tradeoffs and constraints, we will derive two of
151 the most fundamental equations of SDLHT. These equations are not intended to capture
152 the specifics of any particular system, but have much in common with many systems.
153 That is, they are valuable precisely because they apply to no system in particular, but
154 apply to many systems in general and can be tailored to specific biological problems.

155 Throughout, we use a framework in which time is treated discretely for three reasons.
156 First, this avoids the problem of having to decide which kind of stochastic calculus to use
157 (Krener 1979, Mangel 1985). Second, using a discrete time framework from the outset
158 means that the equations we derive are difference rather than differential or partial differ-
159 ential equations. This helps maximize the number of potential users since discrete time
160 equations are already set up for numerical solution by iterative methods. Furthermore,
161 very often the only way that we can solve continuous time models is by discretizing the
162 equations, so that we are essentially skipping an intermediate step. Third, these equa-
163 tions are nonlinear and thus generally require numerical solutions, which can be easily
164 implemented on a desktop computer. The continuous time framework leads to partial
165 differential equations that generally have to be numerically implemented with small but
166 discrete steps in both state and time, so that one is lead back to a discrete time formulation
167 and solution in any case.

168 The fundamental metric of evolution by natural selection is the change in the frequency
169 of genotypes over time. For most problems, instead of genotypes we focus on allele

170 frequencies, but even then the effects of changes of allele frequencies on phenotypic traits
171 are usually too hard to compute or predict, since we still lack fundamental understanding
172 on the genetic architecture of most polygenic traits (Giske et al 2013). So, we use a proxy,
173 refer to it as fitness, and think of it as the expected reproduction or grand-offspring of a
174 focal individual. SDLHT provides evolutionary endpoints and information about peaks,
175 valleys, and the contours of the fitness landscape. When going hiking we appreciate such
176 maps of the natural landscape, even if they are not “realistic” (what good would a 1:1
177 map be?) and the same is true for doing biology.

178 The canonical equations of SDHLT share the following features. We consider a season
179 of length S , with s denoting time within the season³ and the first period of the season
180 $s = 1$. The organism of interest is characterized by a single physiological state, the
181 dynamic variable $X(s)$ at time s , with specific value x . We assume that there is a
182 maximum value x_{max} that the state variable can take and a critical level x_c such that if
183 the state falls below this level, the organism dies. In general starvation is a much more
184 complicated process (e.g. Scharf 2016) but in the spirit of the most general and simple
185 model, we will ignore those complexities.

186 The Canonical Equation of Activity Choice

187 To begin, we assume that the individual does not reproduce between $s = 1$ and $s = S$, and
188 that at the end of this interval has future reproductive success $\Phi(X(S))$ depending upon
189 its state at S . This assumption clearly applies to juveniles during their developmental
190 period, or migrating birds on their feeding grounds. Although we have not specified units
191 for s and S , it is probably helpful to think of S as the length of the non-breeding interval
192 in days and that s is also measured in days.

193 At each time period (e.g. at the start of each day) $s = 1, 2, \dots$ before S , the individual
194 chooses an activity from a collection of possible activities $i = 1, 2, \dots, I$. In the original
195 formulation, we (Mangel and Clark 1986, 1988) called this the patch selection problem
196 and thought of a forager that each morning chooses to either remain in its burrow (safe
197 from predation but losing energy) or forage in one of two patches, one more profitable
198 but riskier than the other⁴.

³In my previous books, we used T and t to represent times, but T is so universally used to represent temperature, that I am keeping it and to avoid confusion using S and s throughout.

⁴Some colleagues find it offensive to consider anything other than looking for food a kind of foraging, but out principle of using mathematical methods to show how things that look wildly different are really the same shows

Each activity, indexed by i , is characterized by 1) its cost α_i ; 2) its rate of mortality per unit time m_i in the sense that the probability of surviving a single period of that activity is e^{-m_i} (see the following box); 3) the probability λ_i of increasing state if this activity is chosen and 4) the increment in state Y_i if that occurs. Thus, if activity i is chosen when $X(s) = x$ the organism survives to time $s + 1$ with probability e^{-m_i} ; with probability λ_i

$$X(s + 1) = x - \alpha_i + Y_i \quad (9)$$

and with probability $1 - \lambda_i$

$$X(s + 1) = x - \alpha_i. \quad (10)$$

199 More properly, we should write that if $X(s + 1)$ in Eqn 9 is greater than x_{max} , then we
200 set it equal to x_{max} and that if $X(s + 1)$ in either Eqn 9 or 10 is less than x_c , then we
201 set it equal to x_c . When writing the computer code to implement these ideas (which we
202 discuss below) this is essential to do – so much so that in Mangel and Clark (1988) we
203 introduced a special mathematical function for it. In this book, however, I will write the
204 equations similar to 9 or 10 and we will keep the understanding about the critical and
205 maximum values in the background.

that we are okay using the same word for apparently different biological phenomena.

The Rate of Mortality and the Probability of Survival

Although I have shown this connection elsewhere (Hilborn and Mangel 1997, Mangel 2006), it is sufficiently important that it appear here, and in a box. Make an effort to understand it. We want to connect the rate of mortality m_i and the probability of survival over a unit interval of time e^{-m_i} .

To do so, we let $q(t)$ denote the probability that an individual alive at time 0 is still alive at time t . Then $q(0) = 1$ by assumption. To be alive at time $t + \Delta t$ the organism has to be alive at time t , which is $q(t)$ and survive from t to $t + \Delta t$. We define the rate of mortality to mean that the probability of surviving from t to $t + \Delta t$ is $1 - m_i \Delta t + o(\Delta t)$, where $o(\Delta t)$ is a mathematical notation meaning “terms that are higher powers of Δt ”, such as $(\Delta t)^2$. If we assume that the probability of surviving to time t and the probability of surviving over the next interval Δt are independent events, then we multiply the probabilities together so that

$$q(t + \Delta t) = q(t)(1 - m_i \Delta t + o(\Delta t))$$

which we re-arrange as

$$\frac{q(t + \Delta t) - q(t)}{\Delta t} = -m_i q \Delta t + \frac{o(\Delta t)}{\Delta t}$$

We now take the limit as $\Delta t \rightarrow 0$; remembering the definition of the derivative for the left hand side and that $o(\Delta t)$ represents higher powers of Δt for the right hand side gives us

$$\frac{dq}{dt} = -m_i q$$

The Rate of Mortality and the Probability of Survival, Continued

Recalling the property of the exponential distribution and that $q(0) = 1$, we conclude that $q(t) = e^{-m_i t}$, so that over a unit time interval, survival is e^{-m_i} , but when you see that, remember that m_i is a rate, with units of 1/time, and that there is a hidden 1, with units of time, in front of the m_i .

Before we leave this box, there are two other important points, both based on the Taylor expansion of the exponential function, i.e. that $e^x = 1 + x + \frac{x^2}{2}$. First, if we Taylor expand the survival probability over a unit time interval, assuming that m_i is small and keep just the first term, we have $e^{-m_i} \approx 1 - m_i$, which is very accurate when m_i is small (check it out yourself). In Mangel and Clark (1988), we wrote the probability of surviving a visit to patch i as $1 - \beta_i$. While m_i can take any value greater than or equal to 0, β_i has to be constrained to be less than 1.

Second, let us think about survival not over the unit interval but over a very short period of time, i.e. $q(\Delta t) = e^{-m_i \Delta t}$. Then the Taylor expansion gives us

$$e^{-m_i \Delta t} = 1 - m_i \Delta t + \frac{1}{2} (m_i \Delta t)^2 = 1 - m_i \Delta t + o(\Delta t)$$

which was our starting point for defining the rate of mortality. We have not just come full circle; we have demonstrated that our approach is self-consistent.

Letting ‘max’ denote that the maximum over activity choices (here $i = 1, \dots, I$) at each time s and \mathcal{E} denote probabilistic expectation, taken over the stochastic processes of survival and incrementing the state, we introduce the fitness function

$$F(x, s) = \max \mathcal{E}[\Phi(X(S)) | X(s) = x] \quad (11)$$

Thus, $F(x, s)$ is the maximum expected reproductive success at time S given that at time s the state is x .

Imagine that we wanted to compute $F(x, s)$ forward in time. We would specify $X(1) = x$, then make an activity choice, from which we would simulate whether the organism survives or not and finds food or not. In this case, when individuals survive, the new state $X(2)$ will be either $x - \alpha_i + Y_i$ or $x - \alpha_i$. From this new state, we once again choose from one of the I activities and compute $X(3)$ for survivors. We have to repeat this process over and over again until $s = S$. At that point, we have one value of the terminal fitness, depending upon the starting point and the activity choices. But if we want to maximize $\Phi(X(S))$ given the initial state x , we have to investigate, for every starting state and all subsequent ones every possible activity choice. Sitting with pen and paper and drawing out the tree of possibilities leads one to conclude that there must be a better way finding the pattern of state dependent activity that maximizes $\Phi(X(S))$ given that the state is x at a previous time s . There is: we compute $F(x, s)$ backwards in time.

In light of the definition in Eqn 11, $F(x, s)$ satisfies the end condition

$$F(x, S) = \Phi(x) \quad (12)$$

This is the key observation: that since we know fitness at the end of the interval, we must reason backwards in time. Furthermore, since a dead individual accumulates no fitness we have the boundary condition $F(x_c, s) = 0$ for every s .

$F(x, s)$ is a dynamical entity, but we only know its final value. Since we know $F(x, S)$, imagine stepping backward one time unit to $s = S - 1$ and that when $X(S - 1) = x$, activity i is chosen. The probability of surviving from $S - 1$ to S and incrementing state is $e^{-m_i} \lambda_i$. Conditioned on those events, the future expected fitness is $F(x - \alpha_i + Y_i, S - 1 + 1) = F(x - \alpha_i + Y_i, S)$ [which is also equal to $\Phi(x - \alpha_i + Y_i)$] so that the future fitness when activity i is chosen, state is incremented, and the organism survives is $e^{-m_i} \lambda_i F(x - \alpha_i + Y_i, S)$. Similar reasoning applies to the case in which state is not incremented.

Thus, future expected fitness if activity i is chosen at time $S - 1$ is $e^{-m_i} [\lambda_i F(x - \alpha_i +$

233 $Y_i, S) + (1 - \lambda_i)F(x - \alpha_i, S)]$. Since $F(x, S - 1)$ is understood to be maximum fitness
 234 taken over activity choice, we conclude $F(x, S - 1) = \max_i e^{-m_i}[\lambda_i F(x - \alpha_i + Y_i, S) +$
 235 $(1 - \lambda_i)F(x - \alpha_i, S)]$. Following this procedure for every value of x allows us to compute
 236 $F(x, S - 1)$. You may find it helpful here to sketch out on paper a diagram (e.g. Marescot
 237 et al 2013) of what we have just proposed (and maybe even try explaining it to a labmate).

Now that we know $F(x, S - 1)$ for every value of x , we step back in time to $s = S - 2$.
 Iterating this argument, we conclude for $s < S$

$$F(x, s) = \max_i e^{-m_i}[\lambda_i F(x - \alpha_i + Y_i, s + 1) + (1 - \lambda_i)F(x - \alpha_i, s + 1)] \quad (13)$$

238 When solving Eqn 13, we generate fitness as a function of state and time, conditioned on
 239 the environment.

240 In addition, because of the maximization step we also produce the optimal behavior
 241 $i^*(x, s)$ for every state and time. These optimal decisions are key in forward Monte Carlo
 242 simulation because it allows us to predict the behavior of populations of individuals.

243 Note that we can write Eqn 13 very compactly by introducing the fitness value of choos-
 244 ing activity i when $X(t) = x$, $V_i(x, s) = e^{-m_i}[\lambda_i F(x - \alpha_i + Y_i, s + 1) + (1 - \lambda_i)F(x - \alpha_i, s + 1)]$,
 245 so that we have $F(x, s) = \max_i [V_i(x, s)]$.

246 Eqn 13 is our first canonical equation of activity choice. It is an equation of Stochas-
 247 tic Dynamic Programming (SDP). The phrase SDP was invented by the mathematician
 248 Richard Bellman (1920-1984) who wrote a series of papers and books in the early 1950s
 249 introducing and explaining the methods (Bellman 1952, 1954, 1956, 1957). However,
 250 the method of dynamic programming is deeply rooted in classical variational problems
 251 of applied mathematics, going back to the work of William Rowan Hamilton and Carl
 252 Gustav Jacobi in the early 19th century (summarized in Courant and Hilbert 1962; also
 253 see Mangel 2015).

254 We will discuss numerical solution of this equation (and other canonical equations) in
 255 a subsequent section.

256

In solving a problem of this sort, the grand thing is to be able to reason backward. That is a very useful accomplishment, and a very easy one, but people do not practise it very much. In the everyday affairs of life it is more useful to reason forward, and so the other comes to be neglected. There are fifty who can reason synthetically, for one who can reason analytically...Let me see if I can make it clearer. Most people, if you describe a train of events to them, will tell you what the result would be. They can put those events together in their minds, and argue from them that something will come to pass. There are few people, however, who, if you told them a result, would be able to evolve from their own inner consciousness what the steps were which led up to that result. This power is what I mean when I talk of reasoning backward, or analytically.

Sherlock Holmes to John H. Watson, M.D.; as reported by Watson in Chapter 7 of “A Study in Scarlet” reprinted in Doyle. A.C. 1970. *The Complete Sherlock Holmes*. Doubleday, NY

258 **One Activity but for Varying Amounts of Time**

Here’s a riff on the canonical equation for activity choice. In deriving Eqns 12 and 13, we assumed that the individual chooses a single activity in each period. An alternative is that there is only activity, and the choice is how much of the period to be active. Bull et al (1996) used such a model to model the dynamics of lipid levels of juvenile Atlantic salmon *Salmo salar*. To modify the canonical equation, we let α_{rest} and α_{active} denote the the metabolic costs per day for an individual who either rests the entire day or is active the entire day. For simplicity, we assume that this is independent of mass. Also for simplicity, we assume that gains from activity are deterministic and that the gain for an entire day of activity is Y . Then if an individual is active for a fraction f of the day, the dynamics of its state are

$$X(s+1) = X(s) - \alpha_{rest}(1-f) - \alpha_{active}f + fY \quad (14)$$

with the critical and maximal levels implicitly understood. If we assume that the rate of mortality is 0 when not active and m per day when active, then the probability of surviving a day in which a fraction f is spent active is e^{-fm} .

Giving the same interpretations to $\Phi(x)$ and $F(x, s)$ as above, the reasoning that lead

to Eqn 13 now leads to

$$F(x, s) = \max_f e^{-f^m} F(x - \alpha_{rest}(1 - f) - \alpha_{active}f + fY, s + 1) \quad (15)$$

259 This is a another version of the canonical equation for activity choice. You might want to
260 pause here and ask how the equation would look if resource gain from activity were not
261 deterministic, but stochastic.

262 The Canonical Equation of Resource Allocation

263 Acquiring and allocating resources are potentially complicated processes (Figure 2), as
264 an organism first accumulates energy and then distributes it to somatic and
265 gonadal tissue, or creates structures that determine three dimensional shape, which may
266 change as environmental conditions change (Boggs 2009). Our approach to such complex
267 situations will be to build up from simpler pieces, beginning with perhaps the simplest
268 allocation problem possible.

269 Instead of building up resources for future fitness assessed at time S , we consider a case
270 in which the organism accumulates reproductive success throughout the season and then
271 dies at time S . This is true for many insects that live for only one season and lay their
272 eggs during one season, with the offspring emerging the following one. Multiple seasons,
273 such as occur for long-lived birds, can be treated by coupling the end of one season with
274 the start of the next (Mangel and Clark 1988, Clark and Mangel 2000).

275 We now interpret $X(s)$ as the resources available for reproduction between s and S
276 and want to predict how they are allocated over time. To do so, suppose that there is a
277 payoff to the individual such that if r resources are used in a period then the increment
278 in lifetime accumulated reproductive success is $f(r)$ where $f(0) = 0$ and $f(r)$ is a concave
279 function (Figure 3)⁵. The important thing with a concave function is that there are
280 diminishing incremental returns from additional use of resources as c increases (i.e. $f(1) >$
281 $f(2) - f(1) > f(3) - f(2)$, etc). We will assume that an opportunity for reproduction
282 occurs with probability η in each period.

283 For example, when the increment in reproductive success is $f(r) = r(1 - (\frac{r}{r_{max}})^\gamma)$, the
284 mother receives the maximum increment when she lays a clutch of size $r^* = \frac{r_{max}}{(1+\gamma_c)^{1/\gamma_c}}$ (it

⁵A concave function $f(x)$ is one in which a line segment between two points on the curve $y = f(x)$ is below the curve. A concave function is one in which the line segment is above the curve. Sigmoidal or S-shaped curves are convex in some places and concave in others.

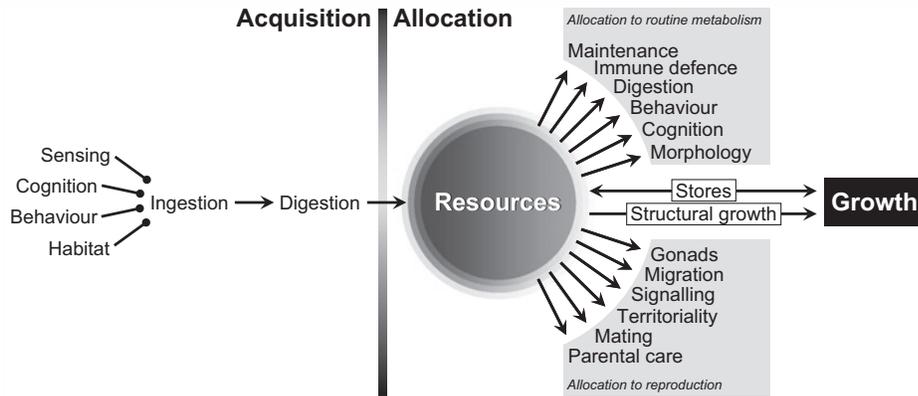
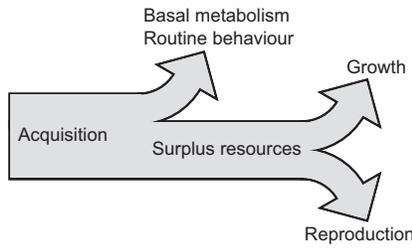


Figure 2: In the simplest view (upper figure), after acquisition resources are allocated to metabolism and behavior, somatic growth, and gonadal stores for reproduction. However (lower figure) acquiring resources and allocating them are both adaptive processes with potentially many sub-components. Figures from Enberg et al (2012).

285 is a nice exercise for you to show this using elementary calculus). We will call this the
 286 Single Host Maximum (SHM) clutch size or Lack Clutch Size (LCS) as a mark of respect
 287 to David Lack, who studied clutch size in birds and pioneered thinking about reproductive
 288 effort (Lack 1947, 1948, 1966). In general, we predict that an individual will lay clutches
 289 of this size or smaller, since a clutch of size greater than r^* will produce a fitness that can
 290 be matched by one smaller than r^* (for an exceptions, see Rosenheim et al (1996)). One
 291 of the questions that we wish to answer is precisely when is she predicted lay clutches
 292 smaller than the SHM clutch.

293

294 We still allow a stochastic increment in resources, which occurs with probability λ in

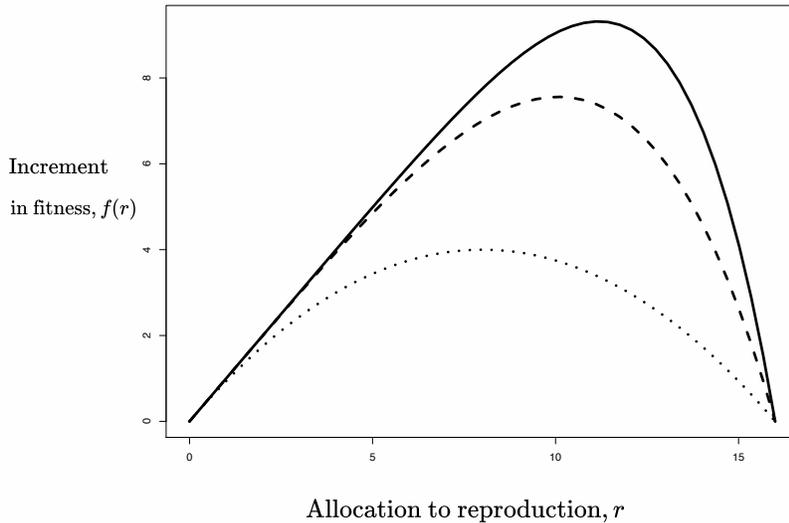


Figure 3: Three examples of increments in fitness $f(c)$ for the canonical equation for resource allocation. They are of the form $f(r) = r(1 - (\frac{r}{16})^\gamma)$ with $\gamma = 1, 3, 5$ for the lowest, middle, and upper curves respectively. A specific insect oviposition analogy is that r is the number of eggs laid in a host and $1 - (\frac{r}{16})^\gamma$ is the probability that an individual offspring survives given that it is a laid in a clutch of size r . The product of these, $f(r)$, is the expected number of surviving offspring. The function $1 - (\frac{r}{16})^\gamma$ is always 0 when $r = 16$ (arbitrarily chosen for this example), and bigger values of γ move the peak further to the right. These functions have a peak at the Single Host Maximum (SHM) clutch size, r_{SHM} .

295 each period and provides an increment R , and a rate of mortality m during each period.
 296 Also for simplicity, we assume that they are constant.

297 The fitness function $F(x, s)$ is now maximum expected accumulated reproductive suc-
 298 cess between s and S given that $X(s) = x$. Assuming that no reproduction occurs at
 299 time S we have the end condition $F(x, S) = 0$ for every x . For previous times, four pos-
 300 sible events occur: i) neither resources nor a reproductive opportunity is encountered, ii)
 301 resources are encountered but no reproductive opportunity is encountered, iii) resources
 302 are not encountered but a reproductive opportunity is encountered, and iv) both re-
 303 sources and a reproductive opportunity are encountered. These occur with probabilities
 304 i) $(1 - \lambda)(1 - \eta)$, ii) $\lambda(1 - \eta)$, iii) $(1 - \lambda)\eta$, and iv) $\lambda\eta$ respectively.

305 Suppose that the current value of the state is x and that if a reproductive opportunity
 306 occurs, r units of resource are used. Then for the cases described above, the state at the
 307 start of the next period will be i) x (since nothing changes), ii) $x + R$ (since resources are

308 augmented but not used), iii) $x - r$ (since resources are not augmented but used), and iv)
 309 $x - r + R$ (since resources are used and augmented). In the last two cases, we cannot allow
 310 more resources than are currently available to be used so that in the allocation decision
 311 we require $r \leq x$. We will also assume that reproduction takes place before survival is
 312 accounted for (if you don't like that assumption, think about how the following equation
 313 will change).

Arguing in analogy to the canonical equation for activity choice, we conclude that $F(x, s)$ satisfies

$$\begin{aligned}
 F(x, s) = & e^{-m}(1 - \lambda)(1 - \eta)F(x, s + 1) + e^{-m}\lambda(1 - \eta)F(x + R, s + 1) \\
 & + (1 - \lambda)\eta \max_{r \leq x} [f(r) + e^{-m}F(x - r, s + 1)] \\
 & + \lambda\eta \max_{r \leq x} [f(r) + e^{-m}F(x - r + R, s + 1)]
 \end{aligned} \tag{16}$$

314 This is the canonical equation for allocation. Note the similarity between Eqns 13 and
 315 16: in both cases we have separated accumulated reproduction from a the age or time
 316 onwards into current reproduction and expected future reproduction. In analogy to the
 317 canonical equation for activity choice, this equation produces two sets of optimal decisions
 318 $r_0^*(x)$ and $r_1^*(x)$, corresponding to the optimal allocation of resources when an reproduc-
 319 tive opportunity arises and no additional resources are encountered or both resources and
 320 a reproductive opportunity are encountered respectively.

321

322 There is also a fundamental difference between Eqns 13 and 16. For the canonical
 323 equation of activity choice, the optimal behavior is determined before any activity is un-
 324 dertaken while in the canonical equation for allocation, optimal behavior is determined
 325 only after a reproductive opportunity is encountered. Eqns 13 and 16 summarize all of
 326 stochastic dynamic programming in biology.

327

I want to focus our attention on the special case of $\lambda = 0$, i.e. there is no increment
 in resources for reproduction during the course of the individual's life as would occur for
 a provigenic parasitoid. In this case, Eqn 16 simplifies to

$$F(x, s) = e^{-m}(1 - \eta)F(x, s + 1) + \eta \max_{r \leq x} [f(r) + e^{-m}F(x - r, s + 1)] \tag{17}$$

328 The solution of Eqn 17 will show us exactly how clutch size will vary over time as a

329 function of the rate of mortality and egg load x .

330 **The Probability Distribution of Behaviors: Errors in Decisions**

331 Recall that we can write the canonical equation for activity choice compactly as $F(x, s) =$
 332 $\max_i [V_i(x, s)]$, where $V_i(x, s) = e^{-m_i}[\lambda_i F(x - \alpha_i + Y_i, s + 1) + (1 - \lambda_i)F(x - \alpha_i, s + 1)]$ is
 333 the fitness value of choosing activity i . Unless there are ties, the solution of this equation
 334 will be a single optimal activity $i^*(x, s)$ for each physiological state and time. But even
 335 when there are not ties, fitness differences may sometimes be very small, and under such
 336 circumstances we would not expect organisms to necessarily follow the optimal activity
 337 choice.

338 To account for both ties and close values of fitness, we use the method of “errors in
 339 decisions” (McNamara et al 1997, Clark and Mangel 2000). We denote fitness of the
 340 optimal activity when $X(s) = x$ by $V^*(x, s)$. Then the fitness difference between the
 341 optimal decision and any other decision $c_i(x, s) = V^*(x, s) - V_i(x, s) \geq 0$, with equality
 342 holding only for the optimal activity.

We assume that the probability $p_i(x, s)$ of choosing activity i when $X(s) = x$ is

$$p_i(x, s) = \frac{e^{-c_i(x,s)/\sigma}}{\sum_{i'=1}^3 e^{-c_{i'}(x,s)/\sigma}} \quad (18)$$

343 where $\sigma > 0$ is a parameter of our choosing. When σ is much bigger than any of the
 344 $c_i(x, s)$, the $p_i(x, s)$ will all be close to $1/3$ – i.e. random decision making. When σ is very
 345 small, then the optimal activity with very high probability⁶.

We now replace Eqns 12 and 13 by

$$\begin{aligned} F(x, S) &= \Phi(x) \\ V_i(x, s) &= e^{-m_i}[\lambda_i F(x - \alpha_i + Y_i, s + 1) + (1 - \lambda_i)F(x - \alpha_i, s + 1)] \\ c_i(x, s) &= V^*(x, s) - V_i(x, s) \\ p_i(x, s) &= \frac{e^{-c_i(x,s)/\sigma}}{\sum_{i'=1}^3 e^{-c_{i'}(x,s)/\sigma}} \\ F(x, s) &= \sum_{i=1}^3 p_i(x, s) V_i(x, s) \end{aligned} \quad (19)$$

⁶Since $c_i(x, s) = V^*(x, s) - V_i(x, s)$, if divide the top and bottom of Eqn 18 by $e^{-V^*(x,s)/\sigma}$ we obtain $p_i(x, s) = \frac{e^{V_i(x,s)/\sigma}}{\sum_{i'=1}^3 e^{V_{i'}(x,s)/\sigma}}$. This formulation is sometimes used, because of its analogy to statistical physics, but it lacks the nice interpretation of the cost of deviation from optimal behavior.

346 If we have observations of activity choice, then we can tune σ by comparing predictions
347 from forward Monte Carlo simulations with the data (e.g. McHuron et al, in press).

348 **Forward Simulation and Behavioral or Life History Observations**

349 After the canonical equations are solved, we have the state and time dependent optimal
350 choices for activity $i^*(x, s)$ or for allocation $r^*(x, s)$. It is these that allow the schedule
351 of survival and reproduction in the Euler-Loka equation to emerge and allow us to make
352 behavioral predictions that can be tested by experiment or observation. To make such
353 predictions, we use Monte Carlo forward simulation in which we simulate a large number
354 of individuals going forward in time, following the optimal behavioral rules.

355 Imagine that we simulate the behavior of K individuals and let $X_k(s)$ denote the state
356 of the k^{th} individual at time s . Since we are going forward in time, we need to specify
357 the initial state of each individual. For example, we might start each individual at i)
358 the maximum state x_{max} , ii) initial state uniformly between the critical value of reserves
359 x_c and the maximum value, iii) initial state normally distributed around a fraction (say
360 80%) of the maximum state, or iv) initial state log-normally distributed around a fraction
361 of the maximum of reserves. Letting \tilde{U} and \tilde{Z}_σ denote a random variable uniformly
362 distributed on $[0,1]$ and normally distributed random variable with mean variance and
363 standard deviation σ , we can write these choices as i) $X_k(1) = x_{max}$, ii) $X_k(1) = x_c +$
364 $(x_{max} - x_c) \cdot \tilde{U}$, iii) $X_k(1) = 0.8 \cdot x_{max} + \tilde{Z}_\sigma$, or iv) $X_k(1) = 0.8 \cdot x_{max} \cdot e^{-\tilde{Z}_\sigma}$.

365 To focus our thinking, consider the canonical equation for resource allocation in which
366 resources are never incremented, so that Eqn 17 applies. After specifying $X_k(1)$ for
367 $k = 1, 2, \dots, 3$, we go forward in time. We first determine if the k^{th} individual encounters a
368 reproductive opportunity. To do so, we draw a random number \tilde{U} uniformly distributed
369 between 0 and 1. If η is greater than or equal to \tilde{U} , then the individual encounters a
370 reproductive opportunity, in which case her reproduction is $r^*(X_k(1), 1)$, where $r^*(x, 1)$
371 is the optimal amount of reproduction determined in the solution of Eqn 17 and her next
372 state is $X_k(2) = X_k(1) - r^*(X_k(1), 1)$. If η is less than \tilde{U} , then she does not encounter
373 a reproductive opportunity, so that $X_k(2) = X_k(1)$. Next, we need to determine if she
374 survives to $s = 2$. Once again we draw a random number uniformly distributed between
375 0 and 1. If this number is less than e^{-m} then she survives to $s = 2$; otherwise she dies
376 at $s=1$. We repeat this procedure until the k^{th} individual dies, runs out of resources for
377 reproduction, or $s = S$.

378 Following this procedure for a single individual does not tell us very much. But if we
379 follow a large number of individuals, at each time s some fraction of the individuals will
380 have survived, providing us with the schedule of survival and some of the survivors will
381 reproduce, providing us with the schedule of reproduction. Thus, the schedule of survival
382 and reproduction that underlie the Euler-Lotka equations emerge from SDLHT.

383 **Numerical Solution of the Canonical Equations**

384 The canonical equations rarely, but sometimes (e.g. Mangel, 1992; Rowe et al 1994),
385 have analytical solutions. However, numerical solution of the SDP equation can provide
386 exceptional insight – both qualitative patterns and detailed numerical predictions. Fur-
387 thermore, by conducting numerical sensitivity analyses we can develop the same kinds
388 of intuition that mathematical analysis often provides. Very often the intuition from a
389 numerical model can be so powerful that one no longer needs the model to understand
390 the phenomenon (Clark 2017).

391 New and deep understanding of the biology of the problem of interest often emerges
392 from building, running, and interpreting the model. This is one of the reasons that Colin
393 Clark and I declined offers to develop software packages for SDP – because you achieve
394 maximum intellectual gain when you do the modeling, since we learn much about the
395 system when making decisions associated with writing the computer program. Of course,
396 a variety of technical issues arise as problems vary, but these can be dealt with as we
397 will explore here and has been done elsewhere (Mangel and Clark 1988, Houston and
398 McNamara 1999, Clark and Mangel 2000).

399 **The Canonical Equation for Activity Choice**

400 In Appendix B, I give code for the backward and forward equations for the canonical
401 equation for activity choice.

402 These codes are intentionally simple and do not take advantage of many of the tools
403 that R offers; doing so makes them accessible to individuals who are new to program-
404 ming in R. Experienced programmers may be annoyed with some of the simplicity; please
405 remember that the codes are intended to be basic. That is okay; you can make them
406 as fancy as you wish. On the other hand, I have found that even experienced program-
407 mers sometimes have difficulty grasping how the SDP algorithm works, so there may be
408 something here for experienced programmers as well. There are now many papers imple-

409 mentoring SDP models, very often with code archived at a stable location so that one can
410 find examples of how things were done by colleagues by searching the web.

411 When preparing this revision, I copied and pasted directly from the Appendix B into R
412 Studio 1.0.143 running R 3.6.1 in the background on an iMac with OS 10.14.6 and confirmed
413 that it works. So, I hope that you are able to copy and paste the pieces directly into R
414 or R Studio and run it without any problems.

415 The first part of the code is just comments, reminding us what it is about and what
416 it is going to do The next part will set the parameters and arrays. The expected gain
417 from activity i is $\bar{Y}_i = \lambda_i \cdot Y_i + (1 - \lambda_i) \cdot 0 = \lambda_i \cdot Y_i$. There is an infinite number of ways
418 to have the same mean gain; how behaviors differ with different choices is worthy of your
419 investigation once the code is running. Next we specify the terminal fitness. For this code,
420 I use $F(x, S) = \frac{x^\gamma}{x^\gamma + c_x x_{max}^\gamma}$ for $x > x_c$ (as always the boundary condition of staying dead
421 applies so that $F(x_c, s) = 0$). There are two parameters, c_x and γ in this end condition.
422 When $c_x = 0$, $F(x, S) = 1$ for $x > x_c$ and 0 otherwise, corresponding to the probability of
423 survival. When $c_x > 0$, $F(x, S)$ will be a saturating function of state and the parameter γ
424 controls how rapidly it rises: when $\gamma > 1$, $\Phi(x)$ is sigmoidal and the larger γ becomes, the
425 more knife-edge $\Phi(x)$ becomes ⁷. We are then ready to iterate backwards in time (this is
426 the essence of the SDP model). Then it is time for some plotting. The code plots i) the
427 end condition first period fitness $F(x, 1)$ as a function of x , ii) level curves of fitness, and
428 iii) activity levels as functions of state and time. The backward iteration is then complete.
429 This gives the optimal decisions; our next step is to code the errors in decisions to give
430 probabilities of different behaviors. We more or less repeat the entire process, but now
431 use the last equation in Eqns 19 to determine fitness.

432 Now we come to the forward iteration. To begin, we need a number of new variables
433 that allow us to track individuals. We now go forward in time. This piece of the code
434 follows individuals in time, tracking their state and who lives and dies (who by fire, who
435 by water, as it were). By doing this we will obtain the distribution of activity over time.
436 We also obtain the total number of individuals, $N_{tot}(s)$, at each time.

Knowing the total number of individuals alive at each time, we can determine the realized rate of mortality m_r by setting

$$N_{tot}(s) = N_{tot}(1)e^{-m_r s} \quad (20)$$

⁷If this is not clear to you, stop reading now and use a spreadsheet, simple computer code, or pencil and paper and explore the function $g(x) = \frac{x^\gamma}{5^\gamma + x^\gamma}$ for x ranging between 0 and 10 and γ ranging between 1 and 8. Ecologists should recognize the case of $\gamma = 1, 2$ as the Holling Type 2 or Type 3 functional responses respectively.

so that a linear fit to the logarithms

$$\log(N_{tot}(s)) = \log(N_{tot}(1)) - m_r s \quad (21)$$

437 has realized mortality as the absolute value of the slope of the line.

438 In Figures 4 and 5 I show respectively the results of the backward iteration and Monte
439 Carlo forward simulation for $c_x = 0$, so that we are considering probability of survival. In
440 Figure 4, first period fitness starts at 0 (which it must, since that corresponds to beginning
441 at the critical value) and rises rapidly leveling off at around $x = 6$, suggesting that there
442 will be strong selection for optimal behaviors for the lower values of x but weaker selection
443 for the higher values. In Figure 5 we see that the realized mortality (panel a) differs from
444 any of the underlying parameter values.

445 In Figures 6 and 7, I show respectively the results of the backward iteration and
446 Monte Carlo forward simulation for $c_x = 0.025$, so that the end condition is sigmoidal.
447 It is instructive to compare results across the two values of c_x . Note, for example, the
448 differences in optimal activity choices (panel b of Figures 4 and 6). The optimal activity
449 choices both figures depend upon both state and time but clearly differ. Think about
450 these for a while and see if you can explain why individuals with $c_x > 0$ are more risk
451 prone than those with $c_x = 0$. (Hint: what is the interpretation of the triangular region
452 in Figure 4b and why does it not appear in Figure 6b?).

453 Comparing Figures 5 and 7, for example, we see that the realized mortality (panels
454 a) when $c_x > 0$ is greater than when it is equal to 0 ; this is consistent with the riskier
455 behavior associated with a sigmoidal terminal fitness. We can track activity choice either
456 by plotting the number of individuals using each activity as a function of time (panels
457 b) or picking jut a few times and plotting the number of individuals using the different
458 activities at those few times (panels c). Think about these for a while and see if you can
459 explain the results.

460 Once you have done that, I suggest that you start to experiment with the code. Do
461 this by changing parameters. I suggest doing so one at a time, and seeing if you can
462 predict what the result will be. This will be time well spent since it will help you develop
463 intuition about the model and its implications.

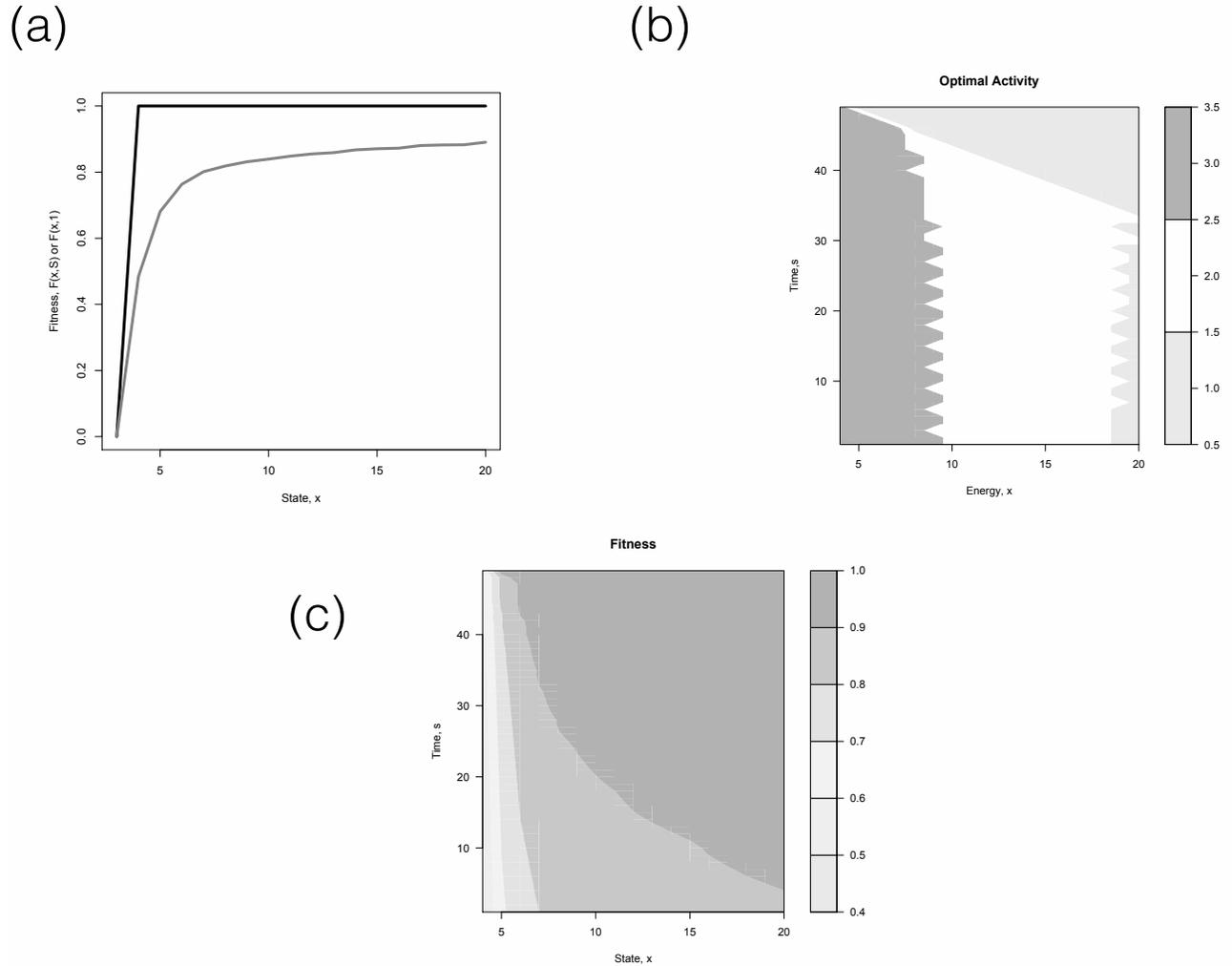


Figure 4: Results from backward iteration of the canonical equation for activity choice with $c_x = 0$ so that the end condition is survival as long as $X(T) > x_{crit}$. a) The terminal fitness function (black line) and first period fitness function (gray line). b) The optimal activity as a function of state and time. Those little saw teeth at either boundary are not numerical errors – they are a fundamental property of the equations of SDP, explained in Reimer et al (2019). c) Filled contours of fitness as function of state and time.

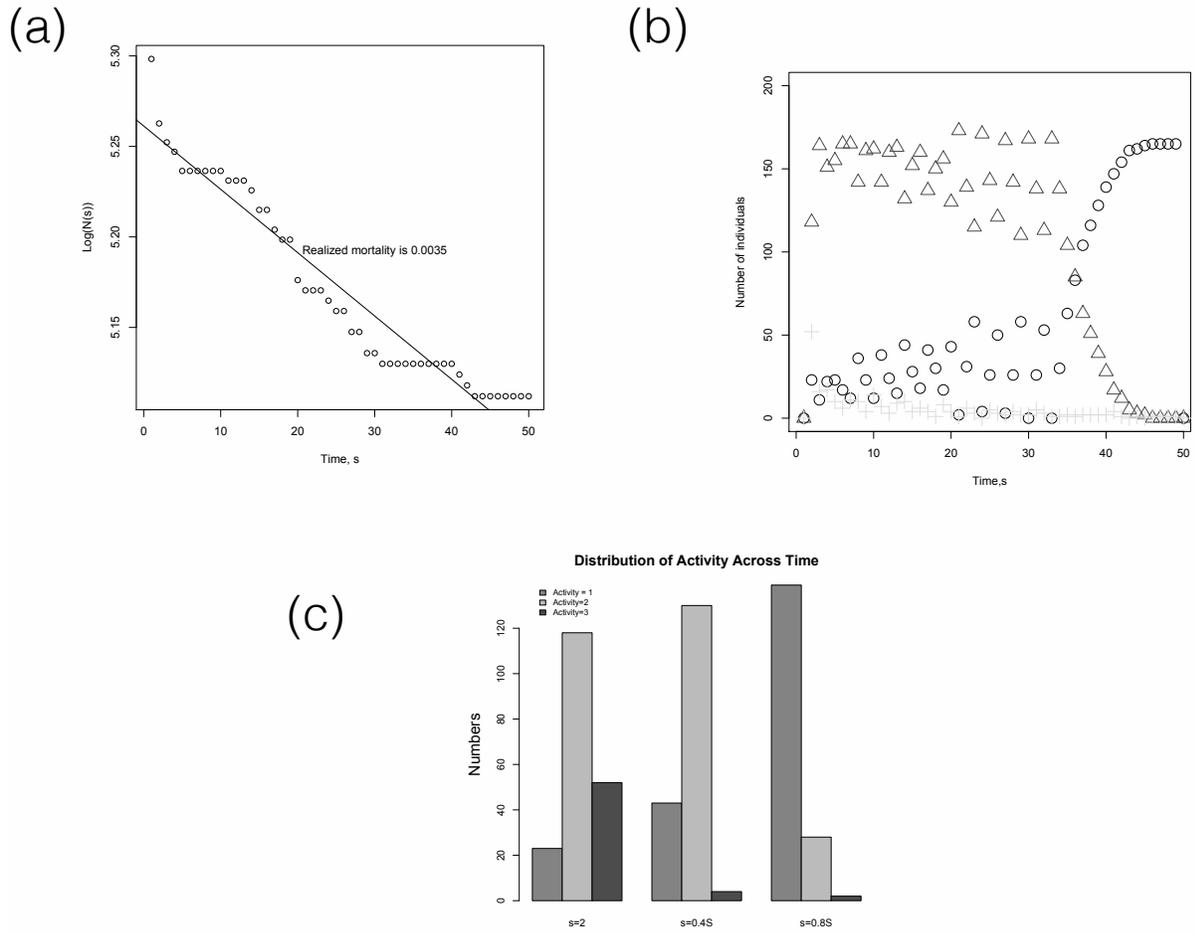
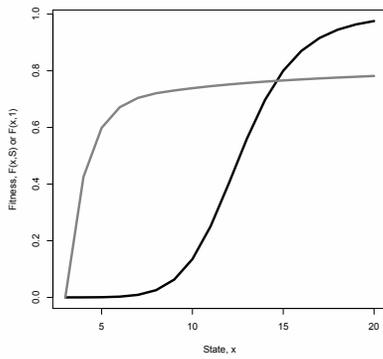
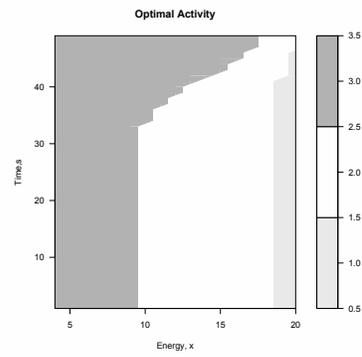


Figure 5: Results from the forward Monte Carlo simulation using the optimal decisions from Figure 4. a) A plot of the logarithm of total population size versus time has slope that is the realized mortality. b) One way of visualizing activity choice is to plot as a function of time the number of individuals using each of the different activities (circles correspond to activity choice 1, triangles to activity choice 2, and crosses to activity choice 3). c) Another way of visualizing activity choice is to show the numbers of individuals following each activity at a few set times.

(a)



(b)



(c)

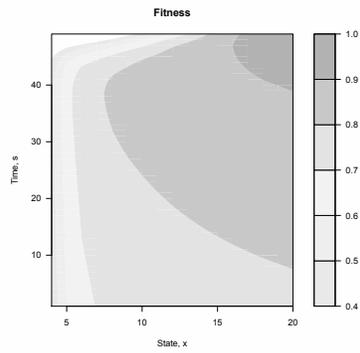


Figure 6: The corresponding results of backward iteration when $c_x = 0.025$. Compare these results with Figure 4.

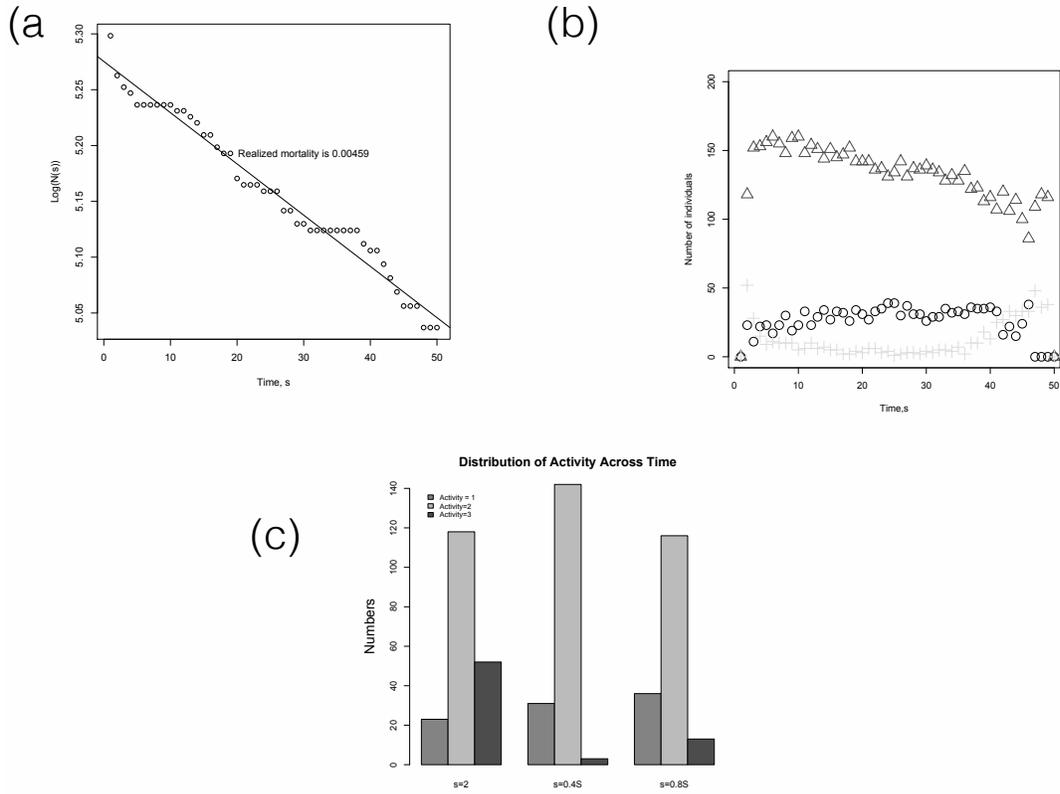


Figure 7: The corresponding results of forward Monte Carol Simulation when $c_x = 0.025$. Compare these results with Figure 5.

464 **Code for the Canonical Equation for Allocation**

465 In Appendix C, I give the R script for the canonical equation for allocation. I wrote
466 the backward iteration to loop over two values of natural mortality, and the forward
467 simulation to use one of those values.

468 That code will produce figures in the spirit of Figure 4-7 (about the canonical equation
469 for activity choice); I encourage you to use it to explore your intuition.

470 **Non-integer Values of State or Time**

471 With these two codes, you already have powerful tools for addressing problems that
472 interest you by tailoring the code to your problem. Here is one technical point.

473 We assumed in the canonical equation for activity choice that all changes in state
474 are integers and in the canonical equation for allocation that time is incremented by
475 one unit, regardless of the level of reproductive activity. But it might be that in the
476 canonical equation for activity choice that either the costs or the increments in state are
477 non-integers, in which case state at the start of the next time period will not be an integer.
478 Similarly, in the canonical equation for allocation, different levels of allocation may take
479 different amounts of time, some of which are non-integers.

480 We will then have non-integer values of entries in the fitness functions on the right
481 hand side of Eqns 13, 16 and 17. One approach is to simply ignore these or to round
482 them; a better approach is to use linear interpolation on the fitness functions; I explain
483 this in Appendix D.

484 **Bioenergetically Based Growth Models**

485 Thus far we have used very simple state dynamics, which allowed us to focus on the
486 development of ideas and methodology without becoming mired in details. The canon-
487 ical equations are powerful because they have much in common with many biological
488 systems while not having high fidelity to any particular one⁸. Even so, there are times
489 when we would like a growth model or an allocation model with more fidelity to nature.

⁸I have not used the word ‘realistic’ because no science – experimental, observational, or theoretical – can ever be realistic in the sense of capturing everything about the world. In order to do science, we forced to exclude some aspects of nature. This is true in experimental work as well as theory (see Caswell (1988) for a nice discussion). I will refer to higher or lower fidelity to nature, using the metaphor of recorded music – which never purports to be live but which we enjoy and respond to, sometimes with great passion.

490 Bioenergetic models capture the sources and sinks of energy allocation in individual or-
 491 ganisms (Kozlowski et al 2004). I will now show how some of the classic models based in
 492 bioenergetics can be linked to the canonical equations for activity choice and allocation.

493 **The von Bertalanffy Growth Model**

The canonical bioenergetic model is due to von Bertalanffy (1957, 1972); also see Sebens (1987) and Mangel (2006). Imagine an organism whose mass at time s is $W(s)$. Mass increases due to anabolic factors (food gathering) and declines due to catabolic factors (metabolism). von Bertalanffy (1957) suggested that we assume food gathering is proportional to surface area and that surface area scales as mass to the $2/3$, so that anabolic factors are written as $aW(s)^{2/3}$, and that metabolism is proportional to volume so that catabolic factors can be written as $bW(s)$. The parameters a and b have units to ensure that both anabolic and catabolic factors have units of *mass/time*. The rate of change of mass is thus

$$\frac{dW}{ds} = aW^{2/3} - bW \quad (22)$$

494 with the initial condition $W(0) = w_0$.

495 Next we assume that mass is related to length $L(s)$ by $W(s) = \rho L(s)^3$. The choice
 496 of 3 as an exponent here is crucial; we have already made this assumption by relating
 497 surface area to mass via a $2/3$ power; a generally useful value is $\rho = 0.01 \text{ g/cm}^3$ although
 498 it varies across species (Froese 2006). In terms of length, anabolic factors are $a\rho^{2/3}L^2$ and
 499 catabolic factors are $b\rho L^3$. Since $\frac{dW}{ds} = \frac{d}{ds}(\rho L^3)$ we the dynamics of length are (applying
 500 the chain rule to the derivative)

$$\rho L^2 \frac{dL}{ds} = a\rho^{2/3}L^2 - b\rho L^3 \quad (23)$$

and a little algebra leads to

$$\frac{dL}{ds} = \frac{a}{3\rho^{1/3}} - \frac{b}{3}L \equiv q - kL \quad (24)$$

where we have defined $q = \frac{a}{3\rho^{1/3}}$ and $k = \frac{b}{\rho}$. Note that if we define $L_\infty = q/k$ then Eqn 24 can also be written as $\frac{dL}{ds} = k(L_\infty - L)$. Eqn 24 is a first order linear differential equation to which we append the initial condition $L(0) = L_0$, and which is solved by either the

method of the integrating factor or writing it as $\frac{dL}{q-kL} = ds$ (Mangel 2006).

The following are equivalent descriptions of von Bertalanffy growth, with $L(0) = L_0$:

$$\frac{dL}{ds} = q - kL \tag{25}$$

$$\frac{dL}{ds} = k(L_\infty - L) \tag{26}$$

$$L(s) = L_\infty(1 - e^{-k(s-s_0)}) \text{ where } L_\infty(1 - e^{ks_0}) = L_0 \tag{27}$$

$$L(s) = \frac{q}{k}(1 - e^{-ks}) + L_0e^{-ks} \tag{28}$$

$$L(s+1) = \frac{q}{k}(1 - e^{-k}) + L(s)e^{-k} \tag{29}$$

501 The units of the left-hand side of Eqn 25 are *length/day*, q must have the same units and
 502 k is a rate with units of $1/day$. Eqn 26 is obtained from Eqn 25 by factoring k through
 503 the right hand side and then defining $L_\infty = \frac{q}{k}$. It is often called the asymptotic size, since
 504 it is the size at which $\frac{dL}{ds} = 0$, which only happens as $s \rightarrow \infty$. Eqn 27 is the solution
 505 of Eqn 24 in which instead of using initial size, we introduce a theoretical time $s_0 < 0$
 506 at which the fish has zero length. Eqn 28 is obtained by solving Eqn 25 with the initial
 507 condition $L(0) = L_0$. Ogle and Isermann (2017) recently argued about the utility of Eqn
 508 28 in fishery management. Finally, Eqn 29 is a special case of Eqn 28 when the time
 509 interval is 1 unit. It will play an important role for us because it links size in one period
 510 with the next. In general, the equations that use $\frac{q}{k}$ rather than L_∞ capture the biology
 511 better because they do not mix the anabolic and catabolic parameters. Kooijman (2000,
 512 pg 223-225) provides a particularly compelling example in which *Daphnia* were grown at
 513 low or high densities of algae and experienced a switch in the density of algae as they
 514 were growing. The apparent asymptotic size shifted according to the food regime. You
 515 might try this yourself with Eqn 29, starting with one value of q , following length as a
 516 function of time and then either increasing or decreasing q at some later point in time. If
 517 you choose to decrease q , think about what it means that organisms shrink in length.

518

519 **Beverton's Theory of Growth, Maturity, and Longevity (GML)**

The great fisheries scientist Ray Beverton (Mangel 2006, pg 25-30) developed a theory of growth, maturity, and longevity based on the von Bertalanffy growth curve. Beverton focussed on age at reproduction. To do so, we append to the growth model in Eqn 27 a rate

of natural mortality m inso that survival to age s is e^{-ms} and assume that reproductive output at age s is $fL(s)^b$. If we assume that the organism is semelparous or iteroparous with no growth after reproduction and identify fitness $\Phi(s)$ with reproduction at age s with expected reproductive output then

$$\Phi(s) = fe^{-ms}L(s)^b \quad (30)$$

Since e^{-ms} starts at 1 when $s = 0$ and declines and $L(s)$ starts at L_0 and then rises to asymptote at q/k , $\Phi(s)$ will be a peaked function of age at reproduction. Thus, we can ask questions about the optimal age at maturity s^* , determined by differentiating $\Phi(s)$ with respect to s , setting the derivative equal to 0, and solving for the optimal age; and about the size at maturity $L(s^*)$. These are (using the L_∞, k form of von Bertalanffy growth)

$$s^* = \frac{1}{k} \log\left(\frac{m + bk}{m}\right) \quad (31)$$

$$L(s^*) = L_\infty \left(\frac{bk}{m + bk}\right) = L_\infty \left(\frac{b}{b + \frac{m}{k}}\right) \quad (32)$$

Eqn 32 tells us that relative size at maturity $\frac{L(s^*)}{L_\infty}$ depends only on the exponent relating size and fecundity and the ratio of m and k , but not their individual values. Furthermore, if we use Eqn 27 with $s_0 = 0$ we obtain

$$L(s^*) = L_\infty(1 - e^{-ks^*}) = L_\infty \left[1 - \exp\left(-\frac{k}{m}ms^*\right)\right] \quad (33)$$

520 from which we conclude that if the relative size at maturity for two species with the same
 521 value of b is the same, then $\frac{m}{k}$ will be the same, so that ms^* will be the same. It is this
 522 kind of observation that lead to the development of the theory of life history invariants
 523 (Charnov 1993, Mangel 1996).

524 **The Canonical Equation for Activity Choice with von Bertalanffy Growth, Version**
 525 **1**

For generalization of the canonical equation for activity choice using von Bertalanffy growth, we let $F(l, s)$ denote the expected reproductive success of an individual with

$L(s) = l$. Then we have the end condition

$$F(l, S) = fl^b \quad (34)$$

526 For previous times, we imagine that there are three kinds of foraging patches characterized
527 by the anabolic parameter (q_i) and the rate of mortality (m_i)⁹.

At any time before S , the organism can either reproduce (and die) or delay reproduction and forage in one of the three patches. The fitness value of reproducing when $L(s) = l$ is $V_R(l) = fl^b$ and the fitness value of visiting patch i is

$$V_i(l, s) = e^{-m_i} F\left(\frac{q_i}{k}(1 - e^{-k}) + le^{-k}, s + 1\right) \quad (35)$$

Consequently, the canonical equation for activity choice will now look like this

$$F(l, s) = \max[V_R(l, s), \max_i\{V_i(l, s)\}] \quad (36)$$

528 **The Canonical Equation for Activity Choice with von Bertalanffy Growth, Version**
529 **2**

We can generalize Eqn 15 when growth is described by the von Bertalanffy formula. If ϕ is the fraction of the day spent foraging, then the probability of surviving the day is $e^{-\phi m}$. Suppose that the state at the start of the day is $L(s) = l$; then in light of Eqn 28, size at the end of the foraging period is $\frac{q}{k}(1 - e^{-\phi k}) + le^{-\phi k}$. After that, size decreases due to metabolism during the rest of the day since in the absence of foraging Eqn 25 corresponds to exponential decay of length¹⁰ Consequently, the fitness value of foraging for a fraction ϕ of the day is

$$V_\phi(l, s) = e^{-\phi m} F(e^{-k(1-\phi)} \left[\frac{q}{k}(1 - e^{-\phi k}) + le^{-\phi k}\right], s + 1) \quad (37)$$

and the generalization of Eqn 15 is

$$F(l, s) = \max[V_R(l, s), \max_\phi\{V_\phi(l, s)\}] \quad (38)$$

⁹Were this a research paper, rather than a tutorial, I would use mass as a state variable with length determined allometrically, and never let length shrink. You might try doing this to see the increase in complexity that arises.

¹⁰It is probably better in this case to track mass, and let individuals lose mass but in most cases not shrink in length. Given the pedagogic nature of start here

The life history application of the von Bertalanffy growth model is particularly simple because it is built on the triple assumptions that anabolic factors scale as mass to the 2/3, mass scales as length cubed, and the organism is semelparous or there is not growth after maturity. It cannot directly apply to iteroparous organisms because growth must change after maturity due to the use of resources for reproduction. This reduction in somatic growth rate arises from energy allocated to reproductive products, but may also include increased costs associated with maintenance of reproductive structures or participation in breeding behavior such as migration (Day and Taylor 1997). We now relax the von Bertalanffy assumptions in order to develop a model for an iteroparous organism with growth after maturity.

Kleiber (1947, 1961) and Brody (1964) suggested that an exponent of 3/4 for anabolic factors and mass; West et al (1999) derive the 3/4 exponent from arguments about the fractal nature of biology. Thus absent reproduction we model growth as

$$\frac{dW}{ds} = aW^{3/4} - bW \quad (39)$$

at least when the organism is not reproducing. We leave the relationship between length and mass unspecified for now because, unlike the case of von Bertalanffy growth in which we used the length-mass relationship to solve the differential equation, we will take a different tack. Eqn 39 needs an initial condition, which is $W(0) = W_0$.

To solve Eqn 39, imagine that there is a function $h(s)$ so that $W(s) = h(s)^4$. Then $h(s) = W(s)^{1/4}$ and $dW/ds = 4h(s)^3 \cdot dh/ds$. This new function allows us to rewrite Eqn 39 as

$$4h^3 \frac{dh}{ds} = ah^3 - bh^4 \quad (40)$$

from which we conclude

$$\frac{dh}{ds} = a/4 - bh \quad (41)$$

with initial condition $h(0) = W_0^{1/4}$. This equation is exactly the same form as Eqn 25, so from Eqn 29 we have

$$h(s+1) = \frac{a}{4b}(1 - e^{-b}) + h(s)e^{-b} \quad (42)$$

We are now ready to use these results in an extension of the canonical equation for allocation.

Next, we need to include mortality and the possibility of per-period reproduction. Rather than use a constant rate of mortality, I will adopt the most general form of size dependent mortality (Lorenzen 2000, Carlson et al 2010, Brodziak et al 2011) in which the rate of mortality per unit time $m(w)$ of an individual whose mass is w is

$$m(w) = m_0 + \frac{m_1}{w^{1/3}} + m_2w \quad (43)$$

The terms on the right hand side respectively account for size-independent mortality, size dependent mortality that decreases as size increase, with the $1/3$ power approximating length (Lorenzen 2000, Brodziak et al 2011) and gape limitation of predators, and size dependent mortality that increases with size due to predators choosing larger individuals. An alternative description of size dependent mortality, which comes from size spectra theory, is described by Andersen (2019).

Now consider an individual whose size at time s is $W(s) = w$. We set $h = w^{1/4}$ and use Eqn 42: if the organism only grows, its mass at the next time period w' is $\left[\frac{a}{4b}(1 - e^{-b}) + he^{-b}\right]^4$. Hence the maximum potential growth in this period is

$$\Delta W(w) = \left[\frac{a}{4b}(1 - e^{-b}) + w^{1/4}e^{-b}\right]^4 - w \quad (44)$$

Now we assume that some of this potential growth is used for reproduction, so that if w_{off} is the mass of a single propagule then when a fraction ϕ of potential growth is used for reproduction, the number of offspring produced is $\frac{\phi\Delta W(w)}{w_{off}}$ and realized reproduction is a function $g\left(\frac{\phi\Delta W(w)}{w_{off}}\right)$, where the function $g()$ accounts for any density dependent survival among the offspring.

We let $F(w, s)$ denote the maximum expected accumulated reproductive success between time s and a final time S , at which reproduction ceases, given that $W(s) = w$. The

generalization of the canonical equation for allocation is

$$F(w, s) = \max_{\phi} \left\{ g \left(\frac{\phi \Delta W(w)}{w_{off}} \right) + e^{-m(w)} F(w + (1 - \phi) \Delta W(w), s + 1) \right\} \quad (45)$$

531 Appendix A: Solution of the Euler-Lotka Equation

532 In this appendix, I describe a method for solving the Euler-Lotka equation, due to Isaac
533 Newton .

We begin with

$$1 = \sum_{a=0}^A e^{-ra} l(a) b(a) \quad (46)$$

and rewrite it as

$$f(r) = \sum_{a=0}^A e^{-ra} l(a) b(a) - 1 = 0 \quad (47)$$

thus defining the function $f(r)$. Suppose that r_{true} , which we don't know, is the solution; that is $f(r_{true}) = 0$. A Taylor expansion of $f(r)$ around this unknown solution gives

$$f(r_{true}) \approx f(r) + f'(r)(r_{true} - r) \quad (48)$$

where $f'(r)$ is the derivative of $f(r)$ with respect to r ; for Eqn 47 it is $f'(r) = -\sum_{a=0}^A a e^{-ra} l(a) b(a)$. By definition, the left hand side of Eqn 48 is 0, and if we re-arrange the right-hand side, solving for r_{true} , we obtain

$$r_{true} \approx r - \frac{f(r)}{f'(r)} \quad (49)$$

This equation is approximate, but suggests the iteration scheme in which we choose r_0 and then define subsequent values by

$$r_{n+1} = r_n - \frac{f(r_n)}{f'(r_n)} \quad (50)$$

534 For the Euler-Lotka equation, the choice $r_0 = 0$, corresponding to a stable population,
535 usually works. We then iterate Eqn 50 until $f(r)$ is as close as we would like it to be.

536 As an exercise, I suggest that you try solving $r^2 = 7.5$ and $r^3 = 8$ using Newton's
537 method; pay attention to how quickly you get to the correct answer.

Appendix B. Code for the Canonical Equation for Activity Choice

```
# R script for the canonical equation for activity choice, written as
#  $F(x,s) = \max_i \{V_i(x,s)\}$  where
#  $V_i(x,s) = \exp(-m_i)[\lambda F(x-\alpha_i+Y_i) + (1-\lambda)F(x-\alpha_i)]$ 

#This code has three parts. 1) The basic SDP. 2) Incorporating errors in decisions # 3) Forward
Monte Carlo Simulation

##### Part 1: The Basic SDP #####

# --- Parameters ---# S = 50
x_max = 20
x_crit = 3

# model time steps
# Maximum energy reserves
# Critical level of reserves (animal dies)

I = 3

# Activity # Activity # Activity # Activity

# number of activities

specific parameters
1 = safe but no energy gain
2 = moderate risk and energy gain, 3 = high risk and energy gain

alpha = c(1,1,1) # energetic cost per timestep of activity i Y = c(0,3,5) # potential energy gained
from activity i lambda = c(0,0.4,0.6) # probability of gaining energy from activity i m =
c(0,0.004,0.02) # risk of mortality from activbity i

# Set the fitness functions and optimal activity
F = array(0,c(x_max,S)) # fitness
V_test = array(0,c(x_max,S,I)) # fitness value of choosing activity i V = array(0,c(I))
i_star=array(0,c(x_max,S)) #optimalactivity

# Specify the Terminal Fitness -- These values for Ch 2 gamma=8
c_x = 0.025

#this value for Ch 7 #gamma=10 #c_x=0.0125
```

```

for(x in x_crit:x_max)
{
  if(x<=x_crit) F[x,S] = 0
  else F[x,S] = x^gamma/(x^gamma+ c_x*x_max^gamma)

  print(c(x,F[x,S]))
}

# -- Next iterate backwards in time. We will loop here rather than vectorize --#

for(s in (S-1):1)      # Loop over time from T-1 to 1
{
  for(x in x_crit:x_max)
  {

    #apply the boundary conditon that F(x_crit,s=0) for all s
    if(x==x_crit)
    {
      F[x,s] = 0
    }
    #otherwise compute the fitness value of each activity
    else
    {
      for(i in 1:I)
      {
        # if activity i leads to a gain in state, the new state is
        # x' = min(x_max, x + Y_i - alpha_i)
        xp = x + Y[i] - alpha[i]
        xp = min(xp,x_max)

        #if activity i does not lead to a gain in state, the new state
        # is x" = max(x_crit, x-alpha[i])
        xpp = x - alpha[i]
        xpp = max(xpp, x_crit)

        #compute the fitness value of visiting this patch
        V_test[x,s,i] = exp(-m[i])* (lambda[i]*F[xp,s+1] + (1-lambda[i])*F[xpp,s+1])
        # V[i]=V_test[x,s,i]
      } #end of the loop over activities

      print(c(s,x,V_test[x,s,]))
    }
  }
}

```

```

# Fitness is the maximum value over all the possible activities

F[x,s] = max(V_test[x,s,])

# determine the optimal activity

i_star[x,s] = which(V_test[x,s,] == max(V_test[x,s,]))
} #end of the check on x
} #end of loop over x
} # end of loop over s

##### Plotting #####

# -- Plot the terminal fitness function and first period fitness --#
quartz()
x_plot = seq((x_crit),x_max,1)
F_plot_S = F[x_plot,S]
F_plot_1 = F[x_plot,1]

plot(x_plot, F_plot_S,type="l",lwd=4, xlab="State, x", ylab="Terminal fitness, F(x,S)")
lines(x_plot,F_plot_1,lwd=4, col=2)

# Plot some level curves #
fit_levels = seq(0.4,1,0.1)
patch_levels = seq(0.5,3.5,1)

x_vals = seq((x_crit+1),x_max,1)
y_vals = seq(1,S-1,1)
F_vals = F[x_vals,y_vals]
p_vals = i_star[x_vals,y_vals]

quartz()

filled.contour(x_vals,y_vals,F_vals,levels = fit_levels,main = "Fitness",xlab="State,
x",ylab="Time, s")

# fit_levels = seq(0.5,1,1.1)
# col=gray(seq(0,0.99,len=length(fit_levels)-1))

```

```
# filled.contour(x_vals,y_vals,F_vals,levels = fit_levels,main = "Fitness",xlab="Energy
(x)",ylab="time(t)",col=gray(seq(0,0.99,len=length(fit_levels)-1)))
```

```
quartz()
filled.contour(x_vals,y_vals,p_vals,levels = patch_levels,main = "Optimal
Activity",xlab="Energy, x",ylab="Time,s")
```

```
***** Part 2 The Probability of Using Different Patches *****
```

```
#decision variable parameter
```

```
sigma=0.02*max(F)
```

```
sigma
```

```
# array for the probabilities that give the probability of using the different
```

```
#patches as a function of state and time
```

```
prob = array(0,c(x_max,S,I))
```

```
#costs
```

```
cost = array(0,c(x_max,S,I))
```

```
#the end condition does not change (per Eqn 2.19)
```

```
for(s in (S-1):1) # Loop over time from T-1 to 1
```

```
{
```

```
  for(x in x_crit:x_max)
```

```
  {
```

```
    #apply the boundary conditon that  $F(x\_crit,s=0)$  for all s
```

```
    if(x==x_crit)
```

```
    {
```

```
      F[x,s] = 0
```

```
    }
```

```
    #otherwise compute the fitness value of each activity
```

```
    else
```

```
    {
```

```
      for(i in 1:I)
```

```
      {
```

```

# if activity i leads to a gain in state, the new state is
#  $x' = \min(x_{\max}, x + Y_i - \alpha_i)$ 
xp = x + Y[i] - alpha[i]
xp = min(xp,x_max)

#if activity i does not lead to a gain in state, the new state
# is  $x'' = \max(x_{\text{crit}}, x - \alpha_i)$ 
xpp = x - alpha[i]
xpp = max(xpp, x_crit)

#compute the fitness value of visiting this patch
V_test[x,s,i] = exp(-m[i])* (lambda[i]*F[xp,s+1] + (1-lambda[i])*F[xpp,s+1])
V[i]=V_test[x,s,i]
} #end of the loop over activities
V_star=max(V)
cost=V_star-V

#make the denominator
denominator=sum(exp(-cost/sigma))
prob=exp(-cost/sigma)/denominator
print(c(s,x,prob))
# Fitness is the maximum value over all the possible activities

F[x,s] = max(V)

# determine the optimal activity

} #end of the check on x
} #end of loop over x
} # end of loop over s

***** Part 3 Forward Simulation
*****

# Need a bunch of parameters

N_ind=200 # number of individuals at the start
N_tot =array(0,c(S)) #total population at time s
s_time=array(0,S)
for(s in 1:S)
{
s_time[s]=s
}

```

```

N_tot[1]=N_ind

X =array(0,c(N_ind,S)) #energy reserves of each individual
# if all initial reserves the same
#random allocation of initial reserves
X[,1]= sample((x_crit+1):x_max,N_ind,replace=TRUE)
#X[,1]=x_crit+2
X[,1]

Activity = array(0,c(N_ind,S)) #current activity

#set the random variables for mortality and finding food outside the loops
set.seed(1000)
mort_rv = replicate(S,runif(N_ind,0,1)) #for mortality
food_rv = replicate(S,runif(N_ind,0,1)) #for increasing reserves
#mort_rv
#food_rv

for(s in 1: (S-1))
{
  for(n in 1:N_ind)
  {

    if(X[n,s]==x_crit) # if the animal was dead last time step, it remains dead!
    {
      X[n,s+1]=x_crit
      Activity[n,s+1] = 0
    }
    else # if the animal was not dead
    {
      i_current = i_star[X[n,s],s]
      print(c(i_current))
      pr_live = exp(-m[i_current])

      # if the organism is not eaten
      if(mort_rv[n,s] < pr_live)
      {
        if(food_rv[n,s] <= lambda[i_current]) # if it finds food
        {
          X[n,s+1] = X[n,s] + Y[i_current] - alpha[i_current]
          if(X[n,s+1] > x_max) X[n,s+1] = x_max # constrain nrg ≤ x_max
        }

        else if(food_rv[n,s] > lambda[i_current])# if they don't find food
        {
          X[n,s+1] = X[n,s] - alpha[i_current]

```

```

    if(X[n,s+1]<=x_crit) X[n,s+1] = x_crit # constrain nrg ≥ x_crit
  }

  if(X[n,s+1] > x_crit) # if they don't die, determine the new patch
  {
    Activity[n,s+1] = i_star[X[n,s+1],s+1]
  }

  else # if they die, set patch to 0
  {
    Activity[n,s+1] = 0
  }
}

# the organism is eaten
else
{
  X[n,s+1] = x_crit
  Activity[n,s+1] = 0
}

} # end the else loop

} # end the n loop

# Calculate total abundance in each timestep
N_tot[s+1] = length(X[X[,s+1]>x_crit,s+1])

} # end the t loop

# plotting

for(s in 1:S)
{
  # N_tot[s]=N_ind*exp(-.01*s)
}

quartz()
#par(mfrow=c(1,2))
plot(s_time, N_tot,xlim=c(1,S))
quartz()
plot(s_time,log(N_tot), xlab="Time, s", ylab="Log(N(s))",xlim=c(1,S))

```

```

lma <-lm(log(N_tot)~s_time)
abline(lma)
cc<-coef(lma)
cc[2]=abs(floor(cc[2]*100000)/100000)
"m"<-toString(cc[2])
legend <-paste("Slope is", toString(cc[2]), sep=" ")
legend
text(0.6*S,0.98*log(N_ind),paste("Realized mortality is", toString(cc[2]), sep=" "))
# #distribution of activity
#
#
N1=array(0,S)
N2=array(0,S)
N3=array(0,S)

for(s in 1:(S-1))
{
  for(n in 1:N_ind)
  {

    if(Activity[n,s]==1)
    {
      N1[s]=N1[s]+1
    }

    if(Activity[n,s]==2)
    {
      N2[s]=N2[s]+1
    }

    if(Activity[n,s]==3)
    {
      N3[s]=N3[s]+1
    }

  }
}
#
quartz()
plot(s_time,N1,type="p",xlim=c(1,(S-1)),pch=1,cex=2.0,xlab="Time,s",ylab="Number of
individuals",ylim=c(0,N_ind) )
points(s_time, N2, col="blue",pch=2,cex=2.0)
points(s_time, N3, col="gold",pch=3,cex=2.0)

```

```

quartz()
par(mfrow=c(2,2))
Dist_act =cbind(N1[2],N2[2],N3[2])
barplot(Dist_act,col="blue",xlab="Activity choice at s=2",ylab="Individuals",
names.arg=c(1,2,3))

```

```

s1=floor(0.4*S)
Dist_act =cbind(N1[s1],N2[s1],N3[s1])
barplot(Dist_act,col="blue",xlab="Activity choice at s=0.4S",ylab="Individuals",
names.arg=c(1,2,3))

```

```

s2=floor(0.8*S)
Dist_act =cbind(N1[s2],N2[s2],N3[s2])
barplot(Dist_act,col="blue",xlab="Activity choice s=0.8S",ylab="Individuals",
names.arg=c(1,2,3))

```

```

# s3=floor(S-2)
# Dist_act =cbind(N1[s3],N2[s3],N3[s3])
# barplot(Dist_act,col="blue",xlab="Activity choice at S-2",ylab="Individuals",
names.arg=c(1,2,3))

```

```

quartz()
Dist_act <- structure(list(W= c(N1[2], N2[2], N3[2]), X = c(N1[s1], N2[s1], N3[s1]), Y =
c(N1[s2], N2[s2], N3[s2])), .Names = c("s=2", "s=0.4S", "s=0.8S" ), class = "data.frame",
row.names = c(NA, -3L))
attach(Dist_act)
print(Dist_act)

```

```

colours <- c("red", "orange", "blue")

```

```

# barplot(as.matrix(Dist_act), main="Distribution of Activity Across Time", ylab = "Numbers",
cex.lab = 1.5, cex.main = 1.4, beside=TRUE, col=colours)
barplot(as.matrix(Dist_act), ylab = "Numbers", cex.lab = 1.5, cex.main = 1.4, beside=TRUE,
col=colours)

```

```

legend(1,142, c("Activity = 1","Activity=2","Activity=3"), cex=0.8, bty="n", fill=colours)

```

Appendix C. Code for the Canonical Equation for Allocation

```
# R script for the canonical equation for allocation
#  $F(x,s) = \exp(-m)(1-\lambda)(1-\eta)F(x,s+1)$ 
#  $+ \exp(-m)\lambda(1-\eta)F(x+R,s+1)$ 
#  $+ (1-\lambda)\eta \max_{\{c \leq x\}} [f(c) + \exp(-m)F(x-c,s+1)]$  #  $+ \lambda\eta \max_{\{c \leq x\}} [f(c) + \exp(-m)F(x-c+R,s+1)]$ 

#This code has two parts. 1) The fundamental SDP. 2) Forward Monte Carlo Simulation #But
each part has sub-parts

##### Part 1: The SDP ##### # --- Parameters ---#

S = 40 # model time steps
x_max = 20 # Maximum energy reserves.
r_max = x_max # Maximum possible level of reproductive effort -- not that we ever expect this
#There is no critical level here but we have to be careful in noting that
#R cannot have 0 as an entry

#Parameters
lambda = 0.1 #probability of incrementing resources (alternative = 0.6) eta = 0.6 # probability of
encountering a reproductive opportunity

#to save writing later on, use p_ij to capture the cases of resources or not, #reproductive
opportunity or no

p_nn = (1-lambda)*(1-eta) #neither resources nor reproduction
p_rn = lambda*(1-eta) #increment resources but no
p_nr = (1-lambda)*eta #do not increment resources but have an opportunity for reproduction p_rr
= lambda*eta #opportunity for incrementing resources and reproduction
print(c(p_nn+p_rn+p_nr+p_rr)) #just a check that we have these right :)

R = 3 #increment in resources when they are encountered; it is worth to explore #R=1 and R=5
also
#m is rate of natural mortality. Determine it by specifying survival to the
#end of the season, surv_end and then solving  $\exp(-m*S) = \text{surv\_end}$ 

#so that  $m = -(1/S)\log(\text{surv\_end})$ 
surv_end = c(0.025, 0.125)
I_m = 2
m = -(1/S)*log(surv_end)
print(c(surv_end, m, exp(-m*S))) #good check that one has done this properly

#need a model for f(r) use that which generated Figure 2.3 with a smaller value #maximum
clutch size
```

```

c_max=10 #reproductive effort leading to no increment in fitness
f_inc=rep(0,(c_max+1))
r=seq(from=0, to=c_max, by=1 )
gamma=2
f_inc=r*(1 - (r/c_max)^gamma)
quartz()
plot(r,f_inc,type="l",lwd=4,xlab="Reproductive allocation, r",ylab="Increment in fitness,f(r)")
points(r,f_inc,cex=2,pch=19)

```

```

# Set the fitness functions and optimal reproductive efforts.
#Being stuck with parasitoids in my mind, I use c for reproductive effort
# R has the annoying feature that 0 cannot be an index. So index state
#by i_x with maximum values I_x
I_x=x_max+1
#max reproductive output is the same, but use a different symbol for clarity
r_max=x_max+1
F = array(0,c(I_x,S)) # fitness
V_test = array(0,c(I_x,S,r_max)) # fitness value of reproductive effort r
V = array(0,c(r_max))
r_star_nr = array(0,c(r_max,S,I_m)) # optimal reproductive effort resources not
#incremented afterwards
r_star_rr = array(0,c(r_max,S,I_m)) # optimal reproductive effort resources
#incremented afterwards
# Specify the Terminal Fitness -- no accumulation after death, so this is very simple

```

```

I_x=x_max+1
for(i_x in 1:I_x)
{
  F[i_x,S] = 0
  x=i_x-1
  #print(c(i_x,x, F[x,S]))
}

```

```

for(i_m in 1:I_m)
{
#Iterate backwards in time
for(s in (S-1):1) # Loop over time from T-1 to 1
{
  for(i_x in 1:I_x)
  {
    #actual value of state
    x=i_x-1
    #Now consider the four possible cases of reproductive opportunities and increasing state

```

```
#If a reproductive opportunity does not occur, there is no behavior
# so that state either stays the same or increases
```

```
#stays the same
```

```
F[i_x,s]=p_nn*exp(-m[i_m])*F[i_x,(s+1)]
```

```
#increases, but cannot exceed maximum value
```

```
x_p = min(x+R, x_max) #new value of state
```

```
i_xp = x_p+1 #new value of index
```

```
F[i_x,s]=F[i_x,s]+p_rn*exp(-m[i_m])*F[i_xp,(s+1)]
```

```
#no increment in resources but a reproductive opportunity.
```

```
max_rep=min(x,c_max)
```

```
V_max=-1
```

```
#i_x=1 implies no eggs, like above
```

```
F[1,s]=p_nr*exp(-m[i_m])*F[1,(s+1)]
```

```
r_star_nr[1,s,i_m]=0
```

```
if(i_x>1)
```

```
{
```

```
  for(i_r in 2:(max_rep+1))
```

```
  {
```

```
    #amount of reproduction
```

```
    r=i_r-1
```

```
    #the fitness increment already accounts for the pesky problem of indexing
```

```
    #need the new state
```

```
    x_p = x - r
```

```
    #print(c(i_x,x,r,x_p+1))
```

```
    s_p=min(s+1,S)
```

```
    i_xp=min(x_p+1,I_x)
```

```
    V_test[i_x,s,i_r] = f_inc[i_r]+ exp(-m[i_m])*F[i_xp,s_p]
```

```
    if(V_test[i_x,s,i_r]> V_max)
```

```
    {
```

```
      V_max= V_test[i_x,s,i_r]
```

```
      r_star_nr[i_x,s,i_m]=r
```

```
      #print(c(s,x,V_max,r_star_nr[i_x,s]))
```

```
    }
```

```
  }#end of loop over possible reproduction
```

```
  # F[x,s]=F[x,s] +p_nr*max(V_test[i_x,s,])
```

```
  F[i_x,s]=F[i_x,s] +p_nr*V_max
```

```
}
```

```
#last case is to have a reproductive opportunity and then increment resources
```

```
#no increment in resources but a reproductive opportunity.
```

```
max_rep=min(x,c_max)
```

```

V_max=-1
#i_x=1 implies no eggs, like above but now increment resources
x_p=1+R
i_xp=x_p+1
F[1,s]=p_rr*exp(-m[i_m])*F[1,(s+1)]
r_star_rr[1,s,i_m]=0
if(i_x>1)
{
  for(i_r in 2:(max_rep+1))
  {
    #amount of reproduction
    r=i_r-1
    #the fitness increment already accounts for the pesky problem of indexing
    #need the new state
    x_p = min(x_max,x - r+R)
    # print(c(i_x,x,r,x_p+1))
    s_p=min(s+1,S)
    i_xp=min(x_p+1,I_x)

    V_test[i_x,s,i_r] = f_inc[i_r]+ exp(-m[i_m])*F[i_xp,s_p]

    if(V_test[i_x,s,i_r]> V_max)
    {
      V_max= V_test[i_x,s,i_r]
      r_star_rr[i_x,s,i_m]=r
      #print(c(s,x,V_max,r_star_nr[i_x,s]))
    }
  }#end of loop over possible reproduction
  #F[i_x,s]=F[i_x,s] +p_rr*max(V_test[i_x,s,])
  F[i_x,s]=F[i_x,s] +p_rr*V_max
}#end of loop over value of state

}#end of loop over state
} #end of loop over time

} #end of loop over m

#look at the output
for(s in 20:20)

```

```

{
  #time_name="Clutch at time "
  #sprintf(%s,time_name)
  for(i_x in 2:I_x)
  {
    x=i_x-1
    print(c(s,x,r_star_nr[i_x,s,i_m],r_star_rr[i_x,s,i_m],1))
  }
}

quartz()
# Make a plot of first period clutches
fpc_nr = array(0,c(I_x,I_m))
fpc_rr = array(0,c(I_x,I_m))
for(i_m in 1:I_m)
{
  fpc_nr[,i_m]=r_star_nr[,1,i_m]
  fpc_rr[,i_m]=r_star_rr[,1,i_m]
}

par(mfrow=c(2,1))
for(i_m in 1:I_m)
{
  plot(fpc_nr[,i_m],xlab="Reserves, x", ylab="First period reproductive effort",ylim=c(0,7))
  points(fpc_rr[,i_m],pch=2,col=2,cex=1.5)
  text(15,1,paste("Rate of mortality m =", toString(floor(1000*m[i_m])/1000), sep=" "))
}

# Now forward simulation, which mimics the forward simulation for the canonical
#equation for activity choice

#Let us use subscript f for environmental variables in the forward simulation
#They could be the same as the ones in the backward, but need not be
lambda_f=lambda #probability of incrementing resources
eta_f=eta # probability of encountering a reproductive opportunity
p_nn=(1-lambda_f)*(1-eta_f) #neither resources nor reproduction
p_rn = lambda_f*(1-eta_f) #increment resources but no
p_nr =(1-lambda_f)*eta #do not increment resources but have an opportunity for reproduction
p_rr =lambda_f*eta_f #opportunity for incrementing resources and reproduction
print(c(p_nn+p_rn+p_nr+p_rr)) #just a check that we have these right :)

R_f=R
S_f=S #to see why these might be different check out Chapter 4
i_m=1
m_f=m[i_m]

```

```

N_ind=500 # number of individuals at the start
N_tot =array(0,c(S)) #total population at time s
s_time=array(0,S)
for(s in 1:S)
{
  s_time[s]=s
}
N_tot[1]=N_ind

X =array(0,c(N_ind,S)) #reproductive reserves of each individual
Current_rep=array(0,c(N_ind,S))
# if all initial reserves the same
#random allocation of initial reserves
X[,1]= sample(0:x_max,N_ind,replace=TRUE)
#X[,1]=x_max
X[,1]

Reproductive_effort = array(0,c(N_ind,S)) #current reproductive effort

#set the random variables for mortality and finding food outside the loops
#set.seed(1000)
#event_rv = replicate(S,runif(N_ind,0,1)) #for finding resources, reproductive opportunities
#mort_rv = replicate(S,runif(N_ind,0,1)) #for mortality

#now go forward in time

for(n in 1:N_ind)
{
  for(s in 1: (S_f-1))
  {
    # print("Working on time, individual")
    # print(c(s,n))

    #only do something if alive
    if(X[n,s]==-1){X[n,s+1]=-1}

    #if alive interesting things can happen
    if(X[n,s]>-1)
    {
      #print("Alive!!")
      i_x=X[n,s]+1
      #which event happened?
    }
  }
}

```

```

event_rv=runif(1,0,1)
#neither food nor reproduction
if(event_rv<=p_nn)
{
#print("Neither food nor resources")
X[n,s+1]=X[n,s]
}#end of neither food nor reproduction

#food but no reproduction
if(event_rv>p_nn)
{
if(event_rv<=p_nn+p_rn)
{
print("Food but no reproduction")
X[n,s+1]=min(X[n,s]+R_f,x_max)
}
}#end of food but no reproduction

#reproduction but no increment in state
if(event_rv>p_nn+p_rn)
{
if(event_rv<=p_nn+p_rn+p_nr)
{
#print("Reproduction but no food")
X[n,s+1]=X[n,s]-r_star_nr[i_x,s,i_m]
i_r=r_star_nr[i_x,s,i_m]+1
Current_rep[n,s]=r_star_nr[i_x,s,i_m]
#Current_rep[n,s]=f_inc[i_r]
}
}#end of reproduction but no food

#final case is both a reproductive opportunity
if(event_rv>p_nn+p_rn+p_nr)
{
X[n,s+1]=min(x_max,X[n,s]-r_star_rr[i_x,s,i_m]+R_f)
#print("Reproduction and resources")
i_r=r_star_rr[i_x,s,i_m]+1
Current_rep[n,s]=r_star_rr[i_x,s,i_m]
#Current_rep[n,s]=f_inc[i_r]
}
}#end of nth individual alive at time s

#decide if this individual dies
mort_rv=runif(1,0,1)
if(mort_rv>exp(-m[i_m]))
{

```

```

    X[n,s+1] =-1
  }

}#end of loop over individuals
}#end of loop over time

#Now some graphics

quartz()
par(mfrow=c(2,2))
for(i_d in 1:4)
{
  s_p=i_d*5 #time at which we will print the histogram
  X_pos=X[,s_p] #select only the individuals who are alive
  X_pos=X_pos[X_pos>-1]
  hist(X_pos,xlab="Reserves, x", ylab="Frequency", main="Resource Distribution")
  mtext(paste("s=", toString(s_p), sep=" "),side=3)
}

quartz()
Total_rep=c(0,c(S)) #total reproductive effort by the population over time
for(s in 1:(S-1))
{
  Total_rep[s]=sum(Current_rep[,s])
}
plot(Total_rep, xlab="Time,s", ylab="Total reproductive effort")

```

538 Appendix D: One and Two Dimensional Linear Interpolation

539 It is common when solving a dynamic programming equation we often have non-integer
540 values of the state x' at the start of the next time period but the fitness function stored in
541 the computer will only accept integer values for its argument. In such a case, I recommend
542 using linear interpolation (Mangel and Clark 1988, Clark and Mangel 2000).

543 One State Variable

544 With one state variable, fitness is $F(x, s)$ where x is the state variable and s is the time
545 variable. Imagine a value x' that is not an integer and we want to know fitness at this
546 value of the state. To determine fitness, we let x_l denote the integer value of state that is
547 closest to but less than x' and $x_u = x_l + 1$ (thus the subscripts denote the integer state
548 just lower than x' and that just above it). The distance between x' and the lower value
549 is $q_x = x' - x_l$, so that when $q_x = 0$, $x' = x_l$ and when $q_x = 1$, $x' = x_u$.

We approximate fitness at x' by assuming that a straight line joins $F(x_l, s)$ and
 $F(x_u, s)$ (Figure 8)

$$F(x', s) \approx q_x F(x_u, s) + (1 - q_x) F(x_l, s) \quad (51)$$

550 Things are a little more complicated in the forward iteration. In general, we will have
551 optimal decisions $d^*(x, s)$ depending upon state and time, but cannot use interpolation to
552 mix decisions when x' is not an integer. In this case, I suggest proceeding as follows. To
553 begin, check to see if $d^*(x_l)$ and $d^*(x_u)$ are the same. If they are, then either can be used
554 for the decision. If they are not, then something else needs to be done. First, one may
555 simply choose to use the decision associated with the lower or upper value of the state or
556 the higher value of fitness. Second, one may choose to use the decision associated with
557 the integer state that is closest to x' . Third, one may randomly choose the state for the
558 decision by drawing a uniformly distribution random number \tilde{U} that ranges between 0
559 and 1 and then comparing it to q_x : if $\tilde{U} > q_x$ then use $d^*(x_l, s)$ and otherwise use $d^*(x_u, s)$.

560 Two (or More) State Variables

The same approach can be used when we have two or more state variables (Figure 9).
We now have stored fitness at discrete values of x and y so that we have $F(x, y, s)$, but
our new state variables x' and y' may not be integers. Proceeding in a manner similar to
one dimension, we let x_l and y_l denote the integers closest to but less than x' and y' and

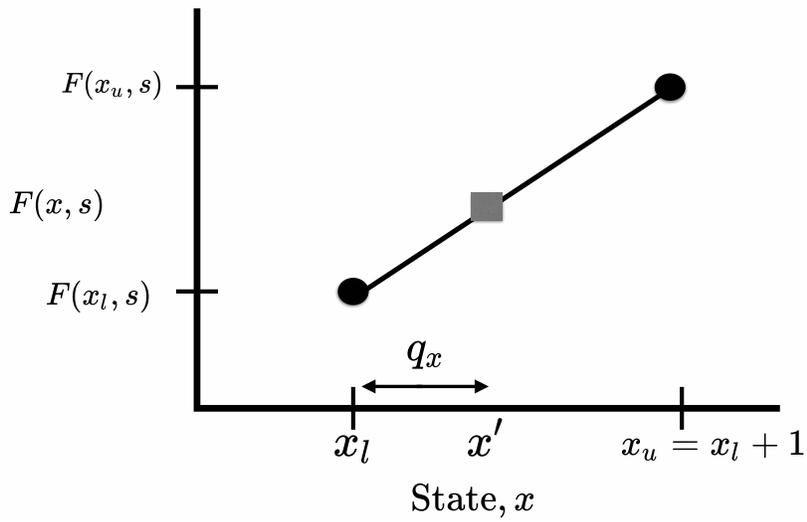


Figure 8: The geometry underlying one dimensional interpolation. We wish to compute fitness at $F(x', s)$, where x' is not integer. We approximate it by assuming that the point $(x', F(x', s))$ lies on the line that joins $(x_l, F(x_l, s))$ and $(x_u, F(x_u, s))$ where x_l and $x_u = x_l + 1$ are the integer values closest to x' but below it and closest to x' but above it.

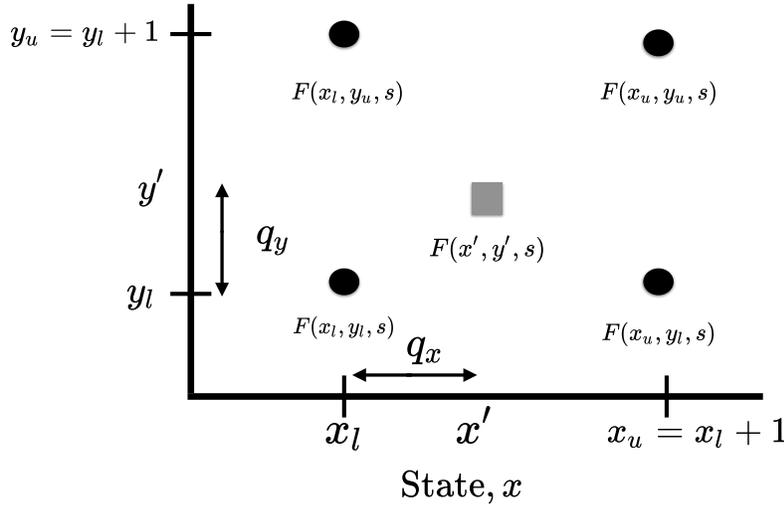


Figure 9: The geometry underlying two dimensional interpolation. Since fitness $F(x, y, s)$ is now a three dimensional function, I am showing the projection onto the $x - y$ plane. To find $F(x', y', s)$ where x' and y' are not integers, we combine $F(x_l, y_l, s)$, $F(x_l, y_u, s)$, $F(x_u, y_u, s)$ and $F(x_u, y_l, s)$, where x_l, x_u, y_l and x_u are defined as above, based on how close the non-integer values of state are to the integer ones.

then set

$$\begin{aligned}
 q_x &= x' - x_l \\
 q_y &= y' - y_l \\
 x_u &= x_l + 1 \\
 y_u &= y_l + 1
 \end{aligned} \tag{52}$$

We now approximate $F(x', y', s)$ by

$$\begin{aligned}
 F(x', y', s) &\approx q_x q_y F(x_u, y_u, s) + (1 - q_x) q_y F(x_l, y_u, s) \\
 &\quad + q_x (1 - q_y) F(x_u, y_l, s) + (1 - q_x)(1 - q_y) F(x_l, y_l, s)
 \end{aligned} \tag{53}$$

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