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1 **Target size and optimal life history when individual growth**
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7 Supplementary material: Figs 2, 3, 4 and 5

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Accepted manuscript

12 **Abstract**

13 I extend my previous work on life history optimization when body mass is divided
14 into reserves and structure components. Two important innovations are: (1) effect of finite
15 target size on optimal structural growth; (2) incorporating reproduction in the optimization
16 objective. I derive optimal growth trajectories and life histories, given that the individual is
17 subject to both starvation mortality and exogenous hazards (e.g., predation). Because of
18 overhead costs in building structural mass, it is optimal to stop structural growth close to the
19 target size, and to proceed only by accumulating reserves. Higher overhead costs cause
20 earlier cessation of structural growth and smaller final structures. Semelparous reproduction
21 also promotes early cessation of structural growth, compared to when only survival to target
22 size is maximized. In contrast, iteroparous reproduction can prolong structural growth,
23 resulting in larger final structures than in either the survival or the semelparous scenarios.
24 Increasing the noise in individual growth lowers final structural mass at small target sizes, but
25 the effect is reversed for large target sizes. My results provide predictions for comparative
26 studies. I outline important consequences of my results to additional important evolutionary
27 questions: evolution of sexual dimorphism, optimization of clutch size and evolution of
28 progeny and adult sizes.

29

30 *Keywords:* diffusion process; energy-predation tradeoff; hazard function; state-dependent life
31 history;

32

33

33 1. Introduction

34 Life history and developmental transitions often require the attainment of some target
35 size. For example, “in a variety of animals and plant species adult size appears to be
36 determined by a size threshold for maturation” (Roff, 2002, p. 201). Developmental
37 transitions in insects and amphibians are dependent upon reaching some critical size (Day
38 and Rowe, 2002; Nijhout, 2003; Mirth and Riddiford, 2007). More generally, such thresholds
39 play a key role in recent approaches to developmental plasticity and phenotypic evolution
40 (West-Eberhard, 2003).

41 Thus, target size is an important life history variable, and should affect optimal life
42 history decisions during growth and development of an individual (e.g., Day and Rowe,
43 2002). In this paper, I study the effect of a given finite target size on optimal life history,
44 when individual growth is stochastic. I employ a dynamic optimization approach (e.g., Perrin
45 and Sibly, 1993; Iwasa, 2000; Irie and Iwasa, 2005), and extend my previous work (Filin,
46 2009), by considering not only survival, but also reproduction, as part of the optimization
47 objective.

48 Following much recent work on size-structured populations and individual growth
49 (e.g., Persson et al., 1998; Kooijman, 2000; Gurney and Nisbet, 2004; Filin, 2009), I divide
50 the total body mass of an individual into a reversibly growing component (hereafter, reserves)
51 and an irreversible component (hereafter, structure). The mass of reserves varies
52 stochastically in time, for example, because of fluctuations in consumption, assimilation and
53 metabolic maintenance. I explore how costs of structural growth, noise level in reserves
54 dynamics, and mode of reproduction (e.g., semelparous or iteroparous), all affect optimal
55 investment in structure *versus* reserves, when the individual is subject to both starvation risk
56 and exogenous mortality. Finally, I discuss how my model and results can be easily applied

57 to a wealth of additional evolutionary problems: evolution of sexual dimorphism, optimal
58 clutch size, and optimal progeny and adult sizes.

59 **2. Effect of target size on life history optimization**

60 *2.1 Basic formulations*

61 I denote structural mass by $z(t)$ and reserves mass by $y(t)$. Total body mass is then $z(t)$
62 + $y(t)$. I define the time-varying maximum of total body mass

$$63 \quad (1) \quad \theta(t) = \max_{t_0 \leq \tau \leq t} [y(\tau) + z(\tau)]$$

64 i.e., the maximal total mass reached up to time t . (Below, I interchangeably refer to θ as total
65 body mass, total mass, or body mass.) Both $\theta(t)$ and $z(t)$ grow irreversibly, i.e., can only
66 increase through time, while $y(t)$ is free to either increase or decrease. Because y represents
67 reserves mass, when $y(t)$ drops to a level a (the *starvation boundary*), the individual dies of
68 starvation. Throughout the rest of this paper I set the starvation boundary to zero (i.e., $a = 0$),
69 to avoid unnecessarily cumbersome notation, and because a nonzero starvation boundary
70 results in only minor modifications (if any) to the expressions presented below (see Appendix
71 B), and does not qualitatively change the general conclusions. Therefore, an individual dies
72 of starvation only after exhausting all of its reserves (i.e., when $y[t]$ hits zero).

73 Following Filin (2009), structural growth occurs only each time a new body mass
74 threshold is reached. In mathematical guise, the irreversibly growing structural mass z is a
75 non-decreasing function of θ , i.e., $z(t) = z[\theta(t)]$. Whenever the organism reaches a new
76 maximum of total mass (i.e., a new, higher value of θ), there can be structural growth
77 associated with this crossing of a new body mass threshold. In addition, structural growth
78 always occurs on the expense of reserves y . A unit of structural mass is built by consuming
79 $1 + \alpha$ units of reserves mass. The dimensionless parameter α represents *overhead costs* of
80 building structural mass.

81 In between events of structural growth (while $\theta[t]$ and thus $z[t]$ remain unchanged),
 82 the dynamics of reserves $y(t)$ is described by a diffusion process on the interval $[0, \theta - z]$. This
 83 diffusion process is characterized by $g(y, z)$ (the *mean growth rate*) and by $\sigma^2(y, z)$ (the
 84 *growth variance*) representing, respectively, the mean balance of input (e.g., assimilation)
 85 and output (e.g., metabolic maintenance) fluxes of energy and mass, and the random
 86 fluctuations around this mean balance. In general, both mean growth rate g and growth
 87 variance σ^2 are dependent on both reserves mass y and structural mass z (but see following
 88 sections). (The units of g are that of [mass/time], while the units of σ^2 are that of
 89 [mass²/time].)

90 In addition to starvation mortality (if $y[t]$ hits the starvation boundary), the individual
 91 is subject to various exogenous hazards (e.g., predation and disease). These are captured by
 92 the mortality or hazard rate $\mu(y, z)$. Survival probability from initial reserves mass y_1 to final
 93 reserves mass y_2 ($\geq y_1$), while keeping z fixed, is given by

$$94 \quad (2) \quad S_y(y_1, y_2) = \exp\left(-\int_{y_1}^{y_2} \eta(y, z) dy\right)$$

95 where $\eta(y, z)$ is the *hazard density*, the hazard function for survivorship through transitions in
 96 the value of reserves mass (i.e., along the y -axis, from a lower value of reserves y_1 to a higher
 97 value y_2). The hazard density η describes mortality per unit of gain in mass (analogously,
 98 mortality rate μ , describes mortality per unit of time, i.e., along the time axis), and
 99 encapsulates within it both starvation mortality and exogenous mortality.

100 In the following, initial body mass of an individual will be denoted by θ_0 and target
 101 body mass by θ_2 (θ_1 will denote the size at which structural growth ceases; see below).
 102 Survival probability from initial total mass θ_0 to final total mass θ_2 , when structural mass
 103 grows according to $z = z(\theta)$, is given by

104 (3)
$$S_{\theta}(\theta_0, \theta_2) = \exp\left(-\int_{\theta_0}^{\theta_2} \eta(\theta - z, z)(1 + \alpha \dot{z}) d\theta\right)$$

105 (Filin, 2009), where \dot{z} stands for $\partial z / \partial \theta$ (hereafter, the dot sign will always stand for derivative
106 with respect to θ). Note that the hazard function for transitions in total mass (i.e., along the θ -
107 axis; the integrand in Eq.[3]) is inflated by a factor $(1 + \alpha \dot{z})$, dependent on rate and overhead
108 costs of structural growth.

109 Finally, the optimization problem consists of finding the optimal form of the
110 structural growth curve, $z^*(\theta)$, that maximizes the following objective function

111 (4)
$$\log F(\theta_0, \theta_2) = -\int_{\theta_0}^{\theta_2} \eta(\theta - z, z)(1 + \alpha \dot{z}) d\theta + \log R(\theta_2, z_2)$$

112 i.e., fitness is given by $F = S_{\theta}R$, namely, survival probability to target size multiplied by a
113 terminal reward obtained at that size. The terminal reward R (e.g., Houston and McNamara,
114 1999, ch. 3; also known as final function; Perrin and Sibly, 1993, appendix therein) depends
115 on target size θ_2 and on structural mass z_2 obtained at this target size.

116 The state variable in this optimization problem is z , with which a costate variable is
117 associated, denoted by λ . The value of the costate variable at each body mass θ between θ_0
118 and θ_2 (i.e. $\lambda[\theta]$), quantifies the benefit of investing in structural growth, compared to just
119 accumulating reserves. For analyzing the effect of target size on the optimal structural growth
120 curve, $z^*(\theta)$, I require the boundary condition for the value of λ at the target size θ_2

121 (5)
$$\lambda(\theta_2) = \frac{\partial \log R}{\partial z_2}$$

122 (Appendix A).

123 In the following sections I derive the optimal structural growth curve for several
124 forms of the objective (fitness) function (Eq. [4]; more precisely, for several forms of the
125 terminal reward R). First, I consider maximization of survival probability to target size (Eq.

126 [3]). This is also the optimization objective in Filin (2009). Later, I extend the analysis to
 127 consider objective functions that include reproduction.

128 *2.2 Maximizing survival probability to target size: optimal cessation of structural growth due*
 129 *to overhead costs*

130 When maximizing survival probability to final size the terminal reward function in
 131 Eq. (4) is $R = 1$. The boundary condition for λ (Eq. [5]) then becomes $\lambda(\theta_2) = 0$. I have
 132 previously studied optimal structural growth for this case (Filin, 2009; Eq. [12] therein).
 133 However, in that study I did not consider the possible effect of a finite target size on the
 134 optimal structural growth curve $z^*(\theta)$ (in effect, θ_2 is taken to be infinite in Filin, 2009).

135 Filin, (2009) showed that when nonzero structural growth occurs (i.e., $z^* > 0$), $z^*(\theta)$
 136 follows a *singular arc* (a term borrowed from dynamic optimization theory; e.g., Perrin and
 137 Sibly, 1993). Along singular arcs the costate variable λ and the structural mass z satisfy the
 138 condition $\lambda(\theta) = \alpha\eta(\theta - z, z)$ (Appendix A). However, because $\lambda(\theta_2) = 0$, this condition can
 139 never be satisfied at the target size, unless there are no overhead costs of building structural
 140 mass (i.e., if $\alpha = 0$; η is always positive, unless growth is completely deterministic, i.e., $\sigma^2 =$
 141 0 , and there are no exogenous hazards, i.e., $\mu = 0$). Therefore, the pair (θ_2, z_2) (where $z_2 =$
 142 $z^*[\theta_2]$) never lies on a singular arc, unless $\alpha = 0$. I conclude that, for finite target size θ_2 and
 143 nonzero overhead costs of structural growth ($\alpha > 0$), the optimal structural growth curve $z^*(\theta)$
 144 always ends with a plateau, along which structural mass remains constant ($z^*[\theta] = z_2$), and
 145 only reserves grow.

146 As we consider increasingly lower body masses below θ_2 , $\lambda(\theta)$ may gradually
 147 increase from its boundary value $\lambda(\theta_2) = 0$ until the condition $\lambda(\theta) = \alpha\eta(\theta - z, z)$ is finally
 148 satisfied at some body mass, denoted by θ_1 ($\leq \theta_2$; the equality may hold only if $\alpha = 0$). At
 149 that point, the optimal growth curve connects with a singular arc, and as we proceed

150 backwards toward even lower values of θ (i.e., $\theta < \theta_l$), the optimal growth curve exhibits
 151 positive structural growth ($\dot{z}^* > 0$). The overall pattern of optimal structural growth is to grow
 152 along the singular arc until θ_l , and then proceed to the target size θ_2 , by switching to only
 153 accumulating reserves. Therefore, θ_l is termed *switching size*.

154 The switching size, in turn, determines the optimal final structural mass achieved by
 155 the growing individual, because $z_2 = z^*(\theta_2) = z^*(\theta_l)$ (and the latter is determined by the
 156 singular arc). Both θ_l and z_2 will change as target size θ_2 varies. I can therefore obtain a
 157 *switching curve* $z_2(\theta_2)$ that determines the value of the optimal final structural mass as a
 158 function of target size. Figure 1a provides specific examples of such switching curves and
 159 optimal structural growth curves for different target sizes. It is important to note that, in
 160 general, the singular arc is also defined for values of θ above the switching size θ_l (diamonds
 161 in Fig.1a). However, given a finite target size, it is optimal to abandon the singular arc once
 162 structural mass has hit the switching curve (i.e., at the switching size).

163 When reserves growth and exogenous mortality depend only on structural mass (i.e.,
 164 g , σ^2 and μ are functions of z only), Filin, (2009) provides the following expression for the
 165 hazard density

$$166 \quad (6) \quad \eta(y, z) = \chi \coth(\chi y) - \varphi$$

167 where

$$168 \quad (7) \quad \chi = \sqrt{\frac{g^2}{\sigma^4} + \frac{2\mu}{\sigma^2}}, \quad \varphi = \frac{g}{\sigma^2}$$

169 are both functions of structural mass z (i.e., $\chi = \chi[z]$ and $\varphi = \varphi[z]$). The quantity χ combines
 170 both starvation risk (decreasing with g and increasing with σ^2) and exogenous hazards
 171 (increasing with μ), to determine the range of values of reserves mass in which starvation is
 172 the predominant cause of mortality (as opposed to exogenous hazards). (This range can be
 173 described by the interval $[0, \chi^{-1}]$.) The quantity φ measures how stochastic/deterministic the

174 reserves dynamics is: when $\varphi \rightarrow \pm\infty$, the growth of reserves mass is practically deterministic,
 175 while when $\varphi \rightarrow 0$ reserves dynamics behaves like Brownian motion. The units of φ , χ and
 176 η are that of $[\text{mass}^{-1}]$.

177 The approach to calculating the switching curve is to solve for the switching size and
 178 target size (θ_1 and θ_2 , respectively), given a value of final structural mass z_2 . For that purpose,
 179 I define the following dimensionless variables

$$180 \quad (8) \quad Y = \chi y, \quad A = \frac{\chi^2}{\chi'}, \quad B = \frac{\varphi'}{\chi'}, \quad \Phi = \frac{\varphi}{\chi}$$

181 where $\varphi' = d\varphi/dz$ and $\chi' = d\chi/dz$ (note the change in the definitions of Y and A , compared to
 182 Filin, 2009). I then derive (Appendix A) the following expression for the switching curve

$$183 \quad (9) \quad f_{tar}(Y_2, A, B) = f_{tar}(Y_1, A, B) - \alpha A (\coth Y_1 - \Phi)$$

184 where the function f_{tar} is defined as $f_{tar}(Y_2, A, B) = (Y - A)\coth Y - BY$. In addition, $Y_2 = \chi(\theta_2 -$
 185 $z_2)$, $Y_1 = \chi(\theta_1 - z_2)$, and χ, A, B and Φ are all evaluated at structural mass $z = z_2$. Because $(\theta_1,$
 186 $z_2)$ lies on the singular arc, Y_1 obeys

$$187 \quad (10) \quad f_{arc}(Y_1, B) = 2(1 + \alpha)A$$

188 where $f_{arc}(Y, B) = [2Y - \sinh(2Y)] + B[\coth(2Y) - 1]$ (the singular arc equation; Eq. (14) in Filin,
 189 2009; using the revised definitions of Y and A in Eq. [8]). I used these expressions (Eqs. [9]
 190 and [10]) to calculate the switching curves and growth trajectories presented in Fig. 1a.

191 2.3 Maximizing expected allocation to reproduction: semelparity and iteroparity

192 Both Filin (2009) and this study, up to this point, have only considered survival
 193 probability as the objective (fitness) function. Clearly, however, a full description and
 194 optimization of a lifecycle must include reproduction as well. The simplest (yet still realistic)
 195 form of introducing reproduction into the optimization objective is choosing the terminal
 196 reward function in Eq. [4] to be $R = \theta_2 - z_2$, i.e., the mass of reserves accumulated at target

197 size, and available for production of progeny. Alternatively, R can describe yield, for
 198 example, in agricultural crops. The role of reserves is now dual, serving as both insurance
 199 against starvation during growth (in addition to providing raw material and fuel for structural
 200 growth), and as the terminal reward gained once target size is achieved. Therefore, in
 201 addition to the overhead costs of structural growth, discussed above, investment in structure
 202 entails an additional cost in term of reduced fecundity or yield. The boundary condition in
 203 Eq. (5) becomes $\lambda(\theta_2) = -1/(\theta_2 - z_2)$.

204 The expression for the terminal reward from the previous paragraph describes
 205 semelparous mode of reproduction. All reserves are utilized in a single burst of reproduction,
 206 causing the individual to die of starvation immediately after. However, if the individual
 207 retains some reserves after reproduction (denoted by y_3) it may survive to reproduce
 208 additional times, i.e., iteroparous mode of reproduction. The individual sacrifices immediate
 209 reproduction (by not utilizing all of its reserves mass in a single reproduction event), for the
 210 sake of surviving to future reproduction events. Thus, the tradeoff between present and future
 211 reproduction (e.g., between fecundity and parental survival; Roff, 2002, pp. 126-150, pp.
 212 188-198) is generated mechanistically in this model, mediated by the value of y_3 (i.e., the
 213 level of reserves retained after reproduction).

214 I adopt here the concept of a *reproduction buffer* (Kooijman, 2000; p. 115), such that
 215 immediately after each reproduction event, reserves mass is y_3 (reproduction buffer emptied),
 216 and subsequent reproduction events occur each time the individual regains reserves mass $\theta_2 -$
 217 z_2 (reproduction buffer full). Survival between reproduction events is then given by $s =$
 218 $S_y(y_3, \theta_2 - z_2)$ (recall that S_y represents survival along reserves mass transitions, while holding
 219 structural mass fixed; Eq. [2]). The expected number of reproduction events is $1/(1-s)$, and
 220 the terminal reward is then $R = (\theta_2 - z_2 - y_3)/(1-s)$. The boundary condition in Eq. (5) becomes

221 $\lambda(\theta_2) = -1/(\theta_2 - z_2 - y_3) + (\partial s/\partial z_2)/(1-s)$. Additional structural growth does not occur after the
 222 individual begins to reproduce (i.e., after reaching θ_2 for the first time; determinate growth).

223 For semelparous reproduction, $\lambda(\theta_2)$ is now negative ($\lambda[\theta_2] = -1/[\theta_2 - z_2]$), compared
 224 with $\lambda(\theta_2) = 0$ when the objective function was survival probability to target size (previous
 225 section). Integrating backwards from target size θ_2 towards lower body masses, $\lambda(\theta)$ would
 226 take longer to reach the singular arc $\lambda(\theta) = \alpha\eta(\theta - z, z)$ (the right-hand-side of this equation is
 227 nonnegative). Therefore, for a given target size, θ_2 , I expect earlier cessation of structural
 228 growth (smaller switching size, θ_l) and smaller final structural mass (z_2), when semelparous
 229 reproduction is taken into consideration in the objective function. The effect of iteroparous
 230 reproduction on the switching curve is less straightforward (see below).

231 The following analysis again concerns the case with reserves growth and exogenous
 232 mortality dependent only on structural mass (i.e., g , σ^2 and μ are functions only of z). For
 233 semelparous reproduction, the expression for the switching curve is

$$234 \quad (11) \quad f_{tar}(Y_2, A, B) + \frac{A}{Y_2} = f_{tar}(Y_1, A, B) - \alpha A(\coth Y_1 - \Phi)$$

235 where again Y_l obeys the singular arc equation (Eq. [10]). Figure 1b demonstrates that,
 236 indeed, structural growth ceases earlier for semelparous reproduction (dotted curves;
 237 compared with the case of maximizing only survival to target size; previous section; solid
 238 curves in Fig. 1b).

239 For iteroparous reproduction, Appendix A provides the expression for the switching
 240 curve. As Fig. 1b demonstrates the switching curve, in this case, has two branches: upper and
 241 lower. Only the upper branch is a solution of the switching curve equation (Appendix A).
 242 Thus, such a solution exists only if the value of the final structural mass z_2 is high enough.
 243 The lower branch of the switching curve represents the additional constraint $\theta_2 \geq z_2 + y_3$ that
 244 must be obeyed in the case of iteroparous reproduction (not surprisingly the lower branch

245 intersects the abscissa axis at $\theta - \theta_2 = -y_3 = -4$ in the case of Fig.1b). When the equality $\theta_2 = z_2$
246 $+ y_3$ holds, we obtain the limit of continuous reproduction. The amount of reserves spent in
247 each reproduction event goes to zero ($\theta_2 - z_2 - y_3 = dy \rightarrow 0$), survival probability between
248 reproduction events goes to one ($s \rightarrow [1 - \eta(y_3, z_2)dy]$; Eq. [2]), and the expected number of
249 reproduction events becomes infinite (the terminal reward is nonetheless finite: $R = [\theta_2 - z_2 -$
250 $y_3]/[1-s] \rightarrow 1/\eta[y_3, z_2]$). From a biological perspective, however, such continuous
251 reproduction, which consists of an infinite number of infinitesimally small progeny, can only
252 be regarded as an approximation, at best. I further consider this issue below in the discussion.

253 3. Discussion

254 In this study, I extended my previous work (Filin, 2009) and considered optimal
255 stopping conditions for structural growth, when individuals must grow to some given finite
256 target size, and when reproduction is included in the optimization objective. I found that even
257 when the optimization objective is maximizing survival to target size (as in Filin, 2009; i.e.,
258 no reproduction) it is optimal to abandon structural growth altogether close to the target size,
259 and to proceed only by accumulating reserves.

260 Only when there are no overhead costs of building structural mass ($\alpha = 0$), is it
261 optimal to keep investing in structure all the way to the target size. The reason is that the
262 individual pays for such overhead losses of reserves in increased mortality, due to the extra
263 time required to regain those lost reserves. Close to the target size, it is optimal to avoid any
264 such losses of reserves mass (and thus instantaneous total body mass $z[t] + y[t]$). In addition,
265 Fig.1a demonstrates that the higher the overhead costs (i.e., higher α), the earlier structural
266 growth ceases and the smaller final structural mass is (see also Figs 2 and 3 in the
267 supplementary material).

268 The effect of reducing the level of noise in the dynamics of reserves (i.e., reducing
269 the growth variance σ^2) is less straightforward. At small target sizes, a lower noise level
270 increases the final structural mass. However, the cessation of structural growth occurs earlier
271 (i.e., at a smaller total body mass), because lower noise levels also promote faster structural
272 growth. At large target sizes the effect is reversed, lower noise levels cause smaller final
273 structural masses (Fig.1a; see also Figs 2 and 3 in the supplementary material).

274 Filin (2009) also found that varying the growth variance may either increase or
275 decrease final structural mass, depending on the function of the structural trait (e.g., foraging-
276 related or defensive). However, the effect of growth variance in this paper is fundamentally
277 different from the one found by Filin (2009). Because target size is, in effect, infinite in Filin
278 (2009), the results described in that work concern the effect of growth variance on the
279 asymptotic structural mass (i.e., at very large total body masses: $\theta \rightarrow \infty$). Here, by contrast, I
280 consider the effect of the growth variance on optimal cessation of structural growth due to a
281 finite target size, and at final structural masses potentially far from the asymptotic value. As
282 discussed above, the signs of these two different effects may in fact be opposite.

283 When I incorporate reproduction into the optimization objective, the results vary
284 depending on whether reproduction is semelparous or iteroparous (Fig. 1b). Semelparous
285 reproduction always causes earlier cessation of structural growth and smaller final structural
286 masses, compared to the case with no reproduction (when survival is the optimization
287 objective). Iteroparous reproduction introduces a new parameter into the model, y_3 , the
288 amount of reserves retained by the individual after a reproduction event. As Fig.1b
289 demonstrates, at very small target sizes (but nonetheless larger than y_3) the switching size is
290 the initial size and there is no structural growth at all throughout the entire lifetime of the
291 individual (the region right of the iteroparity switching curve in Fig.1b). At larger target
292 sizes, cessation of structural growth is delayed, compared to either semelparous reproduction

293 or no reproduction, causing larger final structural mass for a given initial condition (see
294 growth trajectory examples in Fig. 1b). Finally, at even larger target sizes the switching curve
295 for iteroparous reproduction falls below that for no reproduction and asymptotically
296 approaches that of semelparous reproduction.

297 The above qualitative conclusions remain unchanged also when mortality is size-
298 dependent, decreasing with structural mass (see Figs 2b and 3b in the supplementary
299 material). The effect of size-dependent mortality in this case is only quantitative, prolonging
300 structural growth and thus resulting in larger final structural mass. The effects of increased
301 overhead costs or reduced noise level remain qualitatively the same.

302 The growth trajectory examples in Fig. 1b demonstrate that, given identical initial
303 conditions, target size and parameter values (including identical functional forms of g , σ^2 and
304 μ), the reproduction mode (i.e., no reproduction, semelparity or iteroparity) does not affect
305 the growth trajectory itself. The reproduction mode only affects the stopping condition, i.e.,
306 the body mass and structural mass at which structural growth ceases. (Mathematically, that is
307 because the reproduction mode only affects the terminal reward function R in Eq. [4].). This
308 provides an interesting prediction for comparative studies, where closely related species or
309 populations, or even different individuals within the same population, may exhibit different
310 growth patterns, depending on the reproduction mode they adopt (semelparous or
311 iteroparous).

312 A related question is that of sexual dimorphism (this issue was also briefly addressed
313 in the context of deterministic dynamic optimization models in the discussion of Kozłowski
314 and Wiegert, 1987). Because the benefits and costs of body size and structures vary between
315 males and females within a species, the terminal reward function should also depend on sex.
316 As discussed in the previous paragraph, this would affect the stopping condition, i.e., males
317 and females will cease structural growth at different body mass and attain different final sizes

318 of structures. However, early growth and development will be identical. This is a pattern of
319 bimaturation, and in the context of heterochrony, may lead to males, for example, being
320 hypermorphic compared to females (McNamara, 1995; i.e., sexual dimorphism due to
321 differences in timing of developmental transitions between males and females). However, if
322 there are additional sex-specific differences in consumption, assimilation, metabolism or
323 mortality, the optimal growth trajectories of males and females may diverge earlier in life,
324 and before final structural size is attained. When such differences are caused by differences in
325 behavior between males and females (e.g., Rennie et al., 2008), the model may be extended
326 to include reversible behavioral transitions (which can then be optimized separately for males
327 and females), in addition to the irreversible structural growth, as presented and discussed in
328 Filin (2009).

329 As discussed in the previous section, when $\theta_2 = z_2 + y_3$, iteroparous reproduction
330 becomes continuous, consisting of an infinite number of infinitesimally small progeny. There
331 are at least two ways to remedy this biologically questionable result. First, one can define an
332 upper bound $s_{max} < 1$ for the survival probability between reproduction events (i.e., s). As a
333 result, the expected number of reproduction events can never exceed $1/(1-s_{max})$ (which is
334 finite because $s_{max} < 1$). The parameter s_{max} may embody mortality factors during the
335 reproduction event itself, e.g., due to increased susceptibility to predation. (See also Fig. 3 in
336 the supplementary material.)

337 A second more mechanistic way to avoid continuous reproduction is to introduce a
338 minimum nonzero amount of reserves that the individual must expend during each
339 reproduction event. For example, this amount may represent the costs of producing a single
340 egg. Denoting this amount by a_{egg} , the constraint on target size becomes $\theta_2 \geq z_2 + y_3 + a_{egg}$.
341 When the equality holds, the individual reproduces in single eggs, i.e., clutch size is one,
342 rather than continuously as before (if $a_{egg} = 0$). Figure 4 in the supplementary material further

343 explores these modifications. It is important to note that, although not explicitly formulated
344 as part of the model, using this last modification, optimal clutch size arises as a byproduct of
345 the life history optimization within this model. Thus, the theoretical framework presented in
346 this study also addresses this important ecological and evolutionary problem.

347 There exists an analogy between the model described in this paper and dynamic
348 optimization models for optimal size at maturity when season length is finite (Cohen, 1971;
349 Vincent and Pulliam, 1980; Kozłowski and Wiegert, 1986). A comparison with such models,
350 demonstrates that body mass θ is analogous to the time-coordinate in those models. Target
351 size is analogous to season length, and $\theta - \theta_2$ of Fig.1 is analogous to the ‘time-to-go’ until
352 season end, which determines the optimal switch between growth and reproduction in those
353 models. However, growth in those models is deterministic. Therefore, exploring, for
354 example, the effect of noise in growth is not within their scope.

355 This study explored the optimal way to invest in structural growth, starting from some
356 initial condition and finishing at a given final target size. Target size was taken to be a fixed
357 parameter, and growth and life history were optimized under that constraint. Elsewhere I will
358 additionally explore the simultaneous optimization of the endpoints, i.e., of initial and target
359 sizes (e.g., representing optimal progeny and adult sizes, respectively). Kozłowski (1996)
360 previously obtained such optimal initial and adult sizes for a deterministic life history model.
361 The stochastic model in this work enables me to investigate additional questions, such as the
362 effect of noise in the growth of individuals on optimal progeny and adults sizes.

363 Concerning the above discussion of sexual dimorphism and optimal clutch size, optimizing
364 target size itself will enable to explore sexual size dimorphism in the adult (total) body mass,
365 in addition to sexual dimorphism in the allocation between structure and reserves.

366 Optimization of initial and adult sizes will also result in simultaneous optimization of egg
367 size and clutch size, as a_{egg} will no longer be a fixed parameter but will depend on the initial

368 size, subject to optimization. Finally, I am also currently working on an extension of the
 369 model to indeterminate growers

370 In conclusion, the theoretical framework, presented in this study, provides a powerful
 371 tool for addressing a wide variety of life-history and evolutionary questions, under
 372 biologically realistic conditions, including: subjection to both starvation mortality and
 373 exogenous hazards, noise in the dynamics of individual state, and distinction between
 374 reversible and irreversible components of individual size. These two last aspects of the
 375 growth and development of individuals have important implications to evolution of life
 376 history (as well as to population dynamics; Filin, 2009), that have not yet been fully explored
 377 and assessed.

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381 Appendix A: Derivation of the optimal structural growth curve and the switching curve

382 Applying the Pontryagin maximum principle (Intriligator, 1971, pp. 344-348; Perrin
 383 and Sibly, 1993, appendix therein; Perrin et al., 1993), I obtain the Hamiltonian

$$384 \quad H = -\eta(\theta - z, z)(1 + \alpha u) + \lambda u$$

385 where z is the state variable, λ is the costate variable associated with z , and u is the control
 386 variable, defined as $\dot{z} = u$ (recall that the dot sign stands for derivative with respect to θ). The
 387 dynamics of the costate variable is given by

$$388 \quad (\text{A.1}) \quad \dot{\lambda} = -\frac{\partial H}{\partial z} = (1 + \alpha u) \left(\frac{\partial \eta}{\partial z} - \frac{\partial \eta}{\partial y} \right)_{\substack{y=\theta-z \\ z=z^*(\theta)}}$$

389 with boundary condition given by the derivative of the final function (terminal reward R in
 390 Eq. [4]) with respect to the state variable z

391
$$\lambda(\theta_2) = \frac{\partial \log R}{\partial z_2}$$

392 (i.e., Eq. [5]; Intriligator, 1971, p. 348).

393 The switching function for investing in structural mass is given by $\Sigma = \partial H / \partial u$, or

394
$$\Sigma = -\alpha\eta(\theta - z, z) + \lambda$$

395 When $\Sigma = 0$, I obtain singular control, i.e., this is the equation satisfied by a singular arc, to

396 which I refer throughout the main text. Singular control additionally requires $d\Sigma/d\theta = 0$,

397 which results in the general equation for the singular arc presented by Filin, (2009)

398
$$\left[\frac{\partial \eta}{\partial z} - (1 + \alpha) \frac{\partial \eta}{\partial y} \right]_{y=\theta-z} = 0$$

399 (see derivation therein).

400 I confine the analysis, hereafter, to the special case of reserves growth and exogenous

401 mortality dependent only on structural mass z (i.e., Eqs. [6]-[8]). Applying the conclusion that

402 between θ_1 and θ_2 no structural growth occurs (i.e., the optimal control is $u^* = 0$; thus, $z^*(\theta) =$

403 $const = z_2$), Eq. (A.1) becomes

404
$$\dot{\lambda} = \chi' \coth Y - \chi' Y \operatorname{csch}^2 Y + \chi^2 \operatorname{csch}^2 Y - \phi'$$

405 where $Y = \chi y = \chi(\theta - z)$ (Eq. [8]), $\phi' = d\phi/dz$ and $\chi' = d\chi/dz$, all evaluated at $z = z_2$.

406 Integrating from θ_1 to θ_2 gives

407
$$\lambda(\theta_2) = \lambda(\theta_1) + \left[\left(\frac{\chi'}{\chi} \right) Y \coth Y - \chi \coth Y - \left(\frac{\phi'}{\chi} \right) \right]_{Y_1}^{Y_2}$$

408 where $Y_1 = \chi(\theta_1 - z_2)$ and $Y_2 = \chi(\theta_2 - z_2)$. Multiplying both hand sides by χ/χ' , using the

409 definitions of the dimensionless variables in Eq. (8), and recalling that (θ_1, z_2) lies on the

410 singular arc (therefore, $\lambda[\theta_1] = \alpha\eta[\theta_1 - z_2, z_2] = \alpha\chi \coth Y_1 - \alpha\phi$), I finally obtain

411 (A.2)
$$[(Y_2 - A) \coth Y_2 - B Y_2] - \Lambda = [(Y_1 - A) \coth Y_1 - B Y_1] - \alpha A (\coth Y_1 - \Phi)$$

412 where

413 (A.3)
$$\Lambda = \left(\frac{\chi}{\chi'} \right) \lambda(\theta_2)$$

414 And using the definition of f_{tar} in the main text (under Eq. [9]), Eq. (A.2) can be rewritten as

415 (A.4)
$$f_{tar}(Y_2, A, B) - \Lambda = f_{tar}(Y_1, A, B) - \alpha A (\coth Y_1 - \Phi)$$

416 When the objective function is survival probability to final size, $A = 0$, and I obtain

417 Eq. (9). When the objective function includes semelparous reproduction $\lambda(\theta_2) = -1/(\theta_2 - z_2) =$

418 χ/Y_2 . Equation A4 then becomes Eq. (11). For iteroparous mode of reproduction, $\lambda(\theta_2) = -$

419 $1/(\theta_2 - z_2 - y_3) + s'/(1-s)$ (where s' stands for $\partial s/\partial z_2$). The survival probability s between

420 reproduction events is given by

421 (A.5)
$$s = \frac{\sinh Y_3}{\sinh Y_2} \exp[\Phi(Y_2 - Y_3)]$$

422 (the expression for S_y in Eq. (3) of Filin, 2009) where $Y_3 = \chi y_3$ (y_3 is taken to be a fixed

423 parameter of the model). Consequently, $s'/s = \partial \log s / \partial z_2 = Y_3'(\coth Y_3 - \Phi) - Y_2'(\coth Y_2 - \Phi) +$

424 $\Phi'(Y_2 - Y_3)$. Given that $Y_2 = \chi(\theta_2 - z_2)$, and $\Phi = \phi/\chi$, I obtain $(\chi'/\chi)Y_2' = Y_2 - A$ and $(\chi'/\chi)\Phi' =$

425 $B - \Phi$ (using definitions in Eq. [8]). The mass of reserves immediately after a reproduction

426 event is y_3 , and its dimensionless counterpart is $Y_3 = \chi y_3$. Given that y_3 is a fixed parameter,

427 $(\chi'/\chi)Y_3' = Y_3$, and then Eq. (A.3) becomes

428
$$\Lambda = -\frac{A}{Y_2 - Y_3} - \frac{s}{1-s} [(Y_2 - A) \coth Y_2 - B Y_2 + A \Phi + B Y_3 - Y_3 \coth Y_3]$$

429 Finally, by additionally utilizing the definition of f_{tar} , I arrive at the expression for the

430 switching curve in the case of iteroparous reproduction

431 (A.6)
$$\frac{1}{1-s} f_{tar}(Y_2, A, B) + \frac{A}{Y_2 - Y_3} + \frac{s}{1-s} [A \Phi + B Y_3 - Y_3 \coth Y_3] = f_{tar}(Y_1, A, B) - \alpha A (\coth Y_1 - \Phi)$$

432 where s is given by Eq. (A.5).

433 **Appendix B: Modifications for nonzero starvation boundary**

434 For the survival-probability-to-target-size and iteroparous-reproduction scenarios the
 435 expressions are easily modified for nonzero starvation boundary a by redefining Y (Eq. [8])
 436 as

437 (B.1)
$$Y = \chi(y - a)$$

438 Similarly the hazard density in Eq. (6), is given by

439 (B.2)
$$\eta(y, z) = \chi \coth[\chi(y - a)] - \varphi$$

440 Subsequently, the expressions for the switching curves in these cases remain the same (Eqs.
 441 [9] and [10], and Eq. [A.6] in appendix A).

442 For semelparous reproduction, I define \tilde{a} as the amount of reserves that cannot be
 443 utilized for reproduction, once target size is achieved. It may be possible that the amount of
 444 reserves that cannot be utilized for maintenance to avoid starvation, i.e., the starvation
 445 boundary a , can nonetheless be utilized for reproduction (in this case $\tilde{a} \leq a$). In contrast, some
 446 reserves may be utilized for maintenance, but not mobilized for reproduction (in that case $\tilde{a} \geq$
 447 a). Regardless of which case occurs, the terminal reward is $R = \theta_2 - z_2 - \tilde{a}$, and the boundary
 448 condition in Eq. (5) takes the form $\lambda(\theta_2) = -1/(\theta_2 - z_2 - \tilde{a})$. The expression for the switching
 449 curve is then

450 (B.3)
$$f_{tar}(Y_2, A, B) + \frac{A}{Y_2 - \tilde{Y}} = f_{tar}(Y_1, A, B) - \alpha A (\coth Y_1 - \Phi)$$

451 Where $Y_2 = \chi(\theta_2 - z_2 - a)$ and $\tilde{Y} = \chi(\tilde{a} - a)$ (\tilde{Y} can be either positive or negative depending on
 452 which of the two above-mentioned cases occur). Equation (B.3) becomes Eq. (11) if $\tilde{a} = a$
 453 (i.e., if $\tilde{Y} = 0$).

454

455

456

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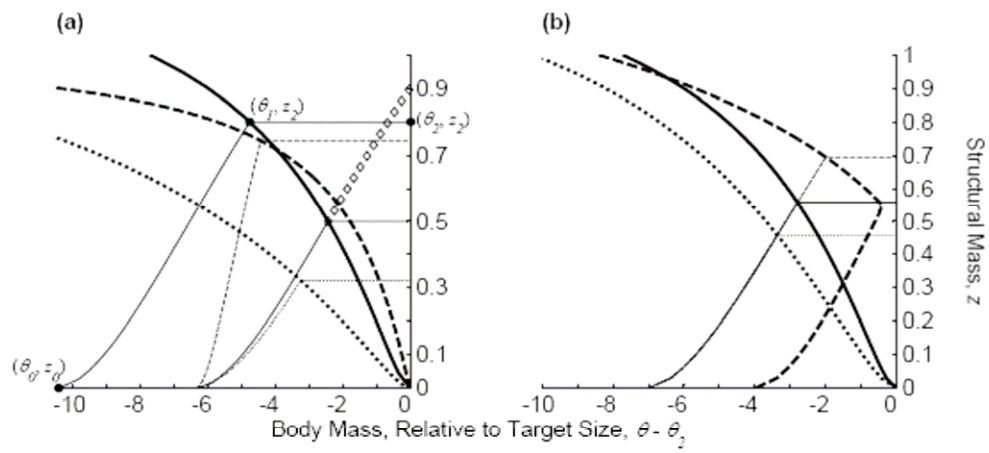
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504 **Figure Legends**

505 **Fig. 1 (a)** Switching curves (thick lines) and sample growth trajectories (thin lines) given:
506 the standard specific model, described below ($\alpha = 1$; solid lines); α is increased to 3 (dotted
507 lines); growth variance σ^2 is uniformly reduced by a factor of 10 (dashed lines). The
508 optimization objective is survival to target size (i.e., no reproduction). In the uppermost
509 sample growth trajectory I marked the points representing (from left to right) the initial size,
510 the switching size and the target size. The other three sample trajectories all emanate from the
511 same initial point. However, because of differences in α or σ^2 both the growth path and the
512 switching size are different. When overhead costs of structural growth (i.e., α) are increased
513 the switching curve becomes lower, but the rate of structural growth is only slightly reduced,
514 causing smaller final structural mass and earlier cessation of structural growth (compare solid
515 with dotted lines). When noise in individual growth is reduced (i.e., σ^2 is reduced), the
516 switching curve is higher for small target sizes, but lower for large target sizes (compare solid
517 and dashed curves). Because a reduced growth variance strongly affects the rate of structural
518 growth, cessation of structural growth occurs earlier, but at higher final structural mass. **(b)**
519 Switching curves and sample growth trajectories for the standard specific model (below),

520 given: no reproduction (solid lines), semelparous reproduction (dotted lines), iteroparous
521 reproduction (dashed lines; $y_3 = 4$). Because in all three cases the values and functional forms
522 of the model parameters are identical (see below), the growth paths are identical (given the
523 same initial condition). The only variation is that structural growth ceases at different body
524 masses (i.e., switching sizes) according to the mode of reproduction. The examples provided
525 in both panels have been obtained using the following standard specific model: $g = 3[z^{2/3} -$
526 $(2/3)z]$, $\sigma^2 = 4(0.1z^{2/3} + 0.9z)$, $\mu = 0.2$, and $\alpha = 1$. The motivation for these specific
527 expressions follows from the work of Kooijman (2000, ch.3), where z here is comparable to
528 Kooijman's *structural volume*. The mean growth rate g is the difference between
529 assimilation, proportional to surface area, and maintenance, proportional to volume. Time
530 and size were rescaled such that maximum mean growth rate is $g = 1$, and it occurs at $z = 1$.
531 The growth variance σ^2 is the sum of noise in assimilation (again proportional to surface
532 area) and noise in maintenance (proportional to structural mass; e.g., representing
533 independent fluctuations in metabolism among cells). Mortality rate is taken to be constant,
534 independent of structural mass (but see online Figs 2 and 3 for examples with size-dependent
535 mortality).
536

536 Fig 1:



537

Accepted