

The effect of starvation on the dynamics of consumer populations

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This is the abstract.

The behavioral ecology of most, if not all, organisms is influenced by the energetic state of individuals, which directly influences how organisms invest reserves in uncertain environments. Such behaviors are generally manifested as trade-offs between investing in somatic maintenance and growth or allocating energy towards reproduction [1, 2, 3]. The timing of these behaviors is often important and is under strong selective pressure, as it tends to directly impact future fitness [4]. Importantly, the influence of resource limitation on an organism's ability to maintain its nutritional stores may lead to repeated delays or shifts in reproduction over the course of an organism's life.

Maximizing fitness between growth and maintenance activities vs. reproduction structures the life-history of many species, and this can be achieved by alternative behavioral strategies conditioned on resource availability [5]. For example, reindeer invest less in calves born after harsh winters (when the mother's energetic state is poor) than in calves born after moderate winters [6], whereas many bird species invest differently in broods during periods of resource scarcity [7, 8], sometimes delaying or foregoing reproduction for a breeding season [1, 9, 10]. Even freshwater and marine zooplankton have been observed to avoid reproduction under nutritional stress [11], with those that do reproduce have lower survival rates [2]. Organisms may also separate maintenance and growth from reproduction over space and time: many salmonids, birds, and some mammals return to migratory breeding grounds to reproduce after one or multiple seasons in alternative environments spent accumulating nutritional reserves [12, 13, 14].

Physiological mechanisms also play an important role in regulating reproductive expenditures during periods of resource limitation. Diverse mammals (47 species in 10 families) exhibit delayed implantation whereby females postpone fetal development (blastocyst implantation) to time with accumulation of nutritional reserves [15, 16], while many others (including humans) suffer irregular menstrual cycling and higher abortion rates during periods of nutritional stress [17, 18]. In the extreme case of unicellular organisms, nutrition is unavoidably linked to reproduction because the nutritional state of the cell regulates all aspects of the cell cycle [19]. The existence of so many independently evolved mechanisms across such a diverse suite of organisms points to the importance and universality of the fundamental tradeoff between somatic and reproductive investment, however the dynamic implications of these constraints are unknown.

Though straightforward conceptually, incorporating the energetic dynamics of individuals [20] into a population-level framework [20, 21] presents numerous mathematical obstacles (in particular a lack of smoothness or differentiability [22]), and is prone to over-fitting. An alternative approach involves modeling the macroscale relationships that guide somatic vs. reproductive investment in a consumer-resource system. Macroscale Lotka-Volterra models assume a dependence of consumer population growth rates on resource density, thus *implicitly* incorpo-

rating the requirement of resource availability for reproduction [23]. Resource limitation and the subsequent effects of starvation may be alternatively accounted for *explicitly*, such that reproduction is permitted only for individuals with sufficient energetic reserves. Such a dynamic introduces *i*) the reproductive time lag associated with changing rates of starvation and recovery, and *ii*) the idea that reproduction is strongly allosterically constrained [3], and not generally linearly related to resource density.

Nutritional state-structured model (NSM)

We explore how the energetic tradeoff between somatic maintenance and growth vs. reproduction can influence population dynamics, and how such dynamics may be constrained by allometry. We begin by establishing a minimal Nutritional State-structured population Model (NSM), where the consumer population is divided into two energetic states: *i*) an energetically replete (full) state F , where the consumer reproduces at a constant rate λ , and *ii*) an energetically deficient (hungry) state H , where reproduction is suppressed, and mortality occurs at rate μ . The resource R has logistic growth with an intrinsic growth rate α and carrying capacity of unity. Consumers transition from state F to state H by starvation at rate σ and in proportion to the lack of resources $(1 - R)$. Conversely, consumers recover from state H to the full state F at rate ρ and in proportion to R . Resources are eliminated by the consumer in both states: by energetically deficient consumers at rate ρ , and by energetically replete consumers at rate β . Accordingly, the system of equations is written

$$\begin{aligned}\dot{F} &= \lambda F + \rho RH - \sigma(1 - R)F, \\ \dot{H} &= \sigma(1 - R)F - \rho RH - \mu H, \\ \dot{R} &= \alpha R(1 - R) - R(\rho H + \beta F).\end{aligned}\quad [0]$$

There are three fixed points associated with the NSM: two trivial fixed points at $(R^* = 0, H^* = 0, F^* = 0)$ and $(R^* = 1, H^* = 0, F^* = 0)$, and one internal fixed point at

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147 implies the simple metabolic balance

$$F^* = \frac{\alpha\lambda\mu(\mu + \rho)}{(\lambda\rho + \mu\sigma)(\lambda\rho + \mu\beta)}, \quad [0]$$

$$H^* = \frac{\alpha\lambda^2(\mu + \rho)}{(\lambda\rho + \mu\sigma)(\lambda\rho + \mu\beta)}, \quad [0]$$

$$R^* = \frac{\mu(\sigma - \lambda)}{\lambda\rho + \mu\sigma}. \quad [0]$$

148 where E'_m is the amount of energy stored in a unit of existing
 149 body mass which may differ from E_m , the energy required to
 150 synthesis a unit of biomass. Give the adult mass, M , of an
 151 organism this energy balance prescribes the mass trajectory of
 152 a starving organism:

$$m(t) = M e^{-B_m t / E'_m}. \quad [0]$$

153 Considering that only certain tissues can be digested for energy,
 154 for example the brain cannot be degraded to fuel metabolism,
 155 we define the rate for starvation and death by the timescales
 156 required to reach specific fractions of normal adult mass. We
 157 define $m_{starve} = \epsilon M$ where it could be the case that organisms
 158 have a systematic size-dependent requirement for essential tis-
 159 sues, such as the minimal bone or brain mass. For example,
 160 considering the observation that body fat in mammals scales
 161 with overall body size according to $M_f = f_0 M^\gamma$, and assum-
 162 ing that once this mass is fully digested the organism begins to
 163 starve, would imply that $\epsilon = 1 - f_0 M^\gamma / M$. Taken together the
 164 time scale for starvation is given by

$$t_\sigma = -\frac{E_m \log(\epsilon)}{B_m}. \quad [0]$$

165 The starvation rate is $\sigma = 1/t_\sigma$, which implies that σ is in-
 166 dependent of adult mass if ϵ is a constant, and if ϵ does scale
 167 with mass, then σ will have a factor of $1/\log(1 - f_0 M^\gamma / M)$.
 168 In either case σ does not have a simple scaling with λ which is
 169 important for the dynamics that we later discuss.

170 The time to death should follow a similar relationship, but
 171 defined by a lower fraction of adult mass, $m_{death} = \epsilon' M$.
 172 Consider, for example, that an organism dies once it has di-
 173 gested all fat and muscle tissues, and that muscle tissue scales
 174 with body mass according to $M_{mm} = mm_0 M^\zeta$, then $\epsilon' =$
 175 $1 - (f_0 M^\gamma + mm_0 M^\zeta) / M$. Muscle mass has been shown to
 176 be roughly proportional to body mass [?] in mammals and thus
 177 ϵ' is effectively ϵ minus a constant. Thus

$$t_\mu = -\frac{E_m \log(\epsilon')}{B_m} \quad [0]$$

178 and $\mu = 1/t_\mu$.

179 The rate of recovery $\rho = 1/t_\rho$ requires that an organism ac-
 180 crues tissue from the starving state to the full state. We again
 181 use the balance given in Equation to find the timescale to re-
 182 turn to the mature mass from a given reduced starvation mass.
 183 The general solution to Equation is given by

$$m(t) = c \left[1 - \left(1 - \frac{b}{a} m_0^{1-\eta} \right) e^{-b(1-\eta)t} \right]^{1/(1-\eta)} \quad [0]$$

184 with $a = B_0/E_m$, $b = B_m/E_m$, and $c = (a/b)^{1/(\eta-1)}$. We are
 185 then interested in the timescale, $t_\rho = t_2 - t_1$, which is the time
 186 it takes to go from $m(t_1) = \epsilon M$ to $m(t_2) = M$, which has the
 187 final form of

$$t_\rho = \frac{\log(1 - (cM)^{1-\eta}) - \log(1 - (ceM)^{1-\eta})}{(\eta-1)b}. \quad [0]$$

188 Although these rate equations are general, here we focus on
 189 parameterizations for terrestrial-bound endotherms, specifically
 190 mammals, which range from $M \approx 1$ gram (the Etruscan shrew
 191 *Suncus etruscus*) to $M \approx 10^7$ grams (the late Eocene to early
 192 Miocene Indricotheriinae). Investigating other classes of organ-
 193 isms requires only substituting the energetic and scale param-
 194 eters shown in Table 1. Moreover, we emphasize that our al-
 195 lometric equations describe mean relationships, and do not ac-
 196 count for the (sometimes considerable) variance associated with
 197 individual species.

198 **The stabilizing effects of allometric constraints**

199 Stability in the NSM is conditioned on the consumer's star- 200 vation rate σ relative to its reproduction rate λ . If $\sigma < \lambda$, 201 the resource steady state density is negative and extinction is 202 inevitable. The condition $\sigma = \lambda$ is a transcritical (TC) bifurca- 203 tion, thus marking a hard boundary below which the system is 204 unphysical due to the unregulated growth of the consumer pop- 205 ulation. That the timescale of reproduction is larger than the 206 timescale of starvation is intuitive for macroscopic organisms, 207 as the rate at which one loses tissue due to a lack of resources 208 is generally much faster than reproduction. In fact, allomet- 209 ric derivations for both reproduction [3] and starvation (Eq.) 210 show that this relationship always holds for organisms within 211 observed body size ranges (Fig. 2). We note that the asymp- 212 tote for the starvation rate at $M \approx 8 \times 10^8$ defines the mass at 213 which body fat accounts for 100% of organismal weight, thereby 214 placing a scaling bound on our derivation for the starvation rate. 215 In addition to the hard bound defined by the TC bi- 216 furcation, oscillating or cyclic dynamics present an implicit 217 constraint to persistence by increasing extinction risk due to 218 stochastic effects. In continuous-time systems, a stable limit cy- 219 cle arises when a pair of complex conjugate eigenvalues crosses 220 the imaginary axis to attain positive real parts [27]. This con- 221 dition, known as a Hopf bifurcation, is defined by $\text{Det}(\mathbf{S}) = 0$, 222 where \mathbf{S} is the Sylvester matrix, which is composed of the coef- 223 ficients of the characteristic polynomial describing the Jacobian 224 [28]. Moreover, as a non-cyclic stable system nears the Hopf bi- 225 furcation, transient or decaying cycles can grow in magnitude, 226 despite the existence of a positive, non-cyclic, steady state den- 227 sity. Given that ecological systems exist in a state of constant 228 population to the hungry state, eliminating reproduction and 229 perturbation [29], even the onset of transient cycles that de- 230 cay over time can increase the risk of extinction [30, 31, 32], 231 such that the distance of a system from the Hopf bifurcation is 232 relevant to persistence.

233 The NSM exhibits both non-cyclic as well as cyclic dynam- 234 ics, and which behavior dominates depends strongly on the rate 235 of starvation σ relative to the rate of recovery ρ . Although 236 starvation leads to mortality risk for the individual, a moder- 237 ate amount promotes persistence of both consumer and resource 238 populations. Non-cyclic stability of the fixed point generally re- 239 quires a higher starvation rate σ relative to the recovery rate ρ . 240 The intuition behind this is that transition to the hungry (non- 241 reproductive) state permits the resource to recover and tran- 242 sient dynamics to subside, whereas a low σ overloads the sys- 243 tem with energetically-replete (reproducing) individuals, thus 244 pletes the consumer population, resulting in a lower steady state 245 density for the consumer and a higher steady state density for 246 the resource.

247 Whereas the rate of consumer growth defines a hard bound 248 of biological feasibility (the TC bifurcation), the rate of starva- 249 tion determines the sensitivity of the consumer population to 250 changes in resource density. While higher rates of starvation 251 result in lower steady state population size – increasing the risk 252 of stochastic extinction – lower rates of starvation result in a 253 system poised near either the TC or Hopf bifurcation (or both), 254 which will lead to elimination of the resource or the develop- 255 ment of cyclic oscillations, respectively. Which bifurcation is 256 approached is wholly dependent on the rate of recovery: if it 257 is high, then cyclic dynamics will develop; if it is low, resource 258 extinction becomes increasingly likely.

259 As the allometric derivations of NSM rate laws reveal, σ 260 and ρ are not independent parameters, such that the bifur- 261 cation space shown in Fig. ?? cannot be freely navigated if 262 assuming biologically reasonable parameterizations. Given the 263 parameterization for terrestrial endotherms shown in Table 1 264 involve potential tradeoffs in reproduction and somatic mainte-

265 with mass M as the only free parameter, rates of starvation 266 and recovery are constrained to a fairly small window of po- 267 tential values (Fig. 4), thus confining dynamics to the steady 268 state regime for all reasonable body size classes. Moreover, for 269 larger M , the distance increases between the allometric values 270 for $\sigma(M)$ and $\rho(M)$ relative to the Hopf bifurcation, while un- 271 physical due to the unregulated growth of the consumer pop- 272 ulation. That the timescale of reproduction is larger than the 273 mean; Fig. 4) results in little difference in the position of the 274 TC and Hopf bifurcations as well as consumer energetic rates. 275 This result suggests 1) that small mammals are more prone to 276 is suggestive of a dynamic barrier to the mass of endothermic 277 organisms. 278

279 Allometric constraints have been invoked to explain the pe- 280 riodicity of cyclic populations [33, 34, 35], such that period 281

282 $\propto M^{0.25}$, however this relationship seems to hold only for some 283 species [36] and competing explanations exist [37, 38]. Though 284 statistically significant support for the existence of population 285 cycles among mammals is based on data for smaller body sized 286 organisms [39], we acknowledge that absence of evidence for 287 cyclic dynamics for longer-lived species is not necessarily evi- 288 dence of absence. We thus obtain a specific prediction from our 289 model: population cycles should be less common among larger 290 species and more common for smaller species, particularly in en- 291 vironments where resources are limiting, emphasizing the role 292 of starvation on dynamics.

293 Higher rates of starvation results in a larger flux of the 294 population to the hungry state, eliminating reproduction and 295 increasing the likelihood of mortality, however it is the rate 296 of starvation relative to the rate of recovery that determines 297 the long-term dynamics of the system (Fig 3). By examin- 298 ing the ratio σ/ρ , we can understand the competing effects of 299 cyclic dynamics vs. steady state density on extinction risk. We 300 computed the probability of extinction, where extinction is de- 301 fined as $H(t) + F(t) = 10$ at any instant across all values of 302 t from $10^3 < t \leq 10^6$, for 1000 replicates of the continuous-time sys- 303 tem shown in Eq. for an organism of $M = 100$ grams, assuming 304 random initial conditions around the steady state (Eq.). By 305 allowing the rate of starvation to vary, we assessed extinction 306 risk across a range of values for the ratio σ/ρ varying between 307 10^{-2} to 2.5, thus examining a horizontal cross-section of Fig. 3. As expected, higher rates of extinction correlated with both 309 low and high values of σ/ρ ; for low values the higher extinction 310 risk results from transient cycles with larger amplitudes as the 311 system nears the Hopf bifurcation (Fig. 5). For large values of 312 σ/ρ , higher extinction risk is due to the decrease in the steady 313 state consumer population density. This interplay creates an 314 ‘extinction refuge’ as shown in Fig. 5, such that for a relatively 315 small range of σ/ρ , extinction probabilities are minimized.

316 As has been described, the σ vs. ρ space cannot be freely 317 traversed, such that not all values of σ/ρ are biologically fea- 318 sible. We observe that the allometrically constrained values of 319 σ/ρ (with $\pm 20\%$ variability around energetic parameter means) 320 fall within the extinction refugia, such that they are close 321 enough to the Hopf bifurcation to avoid low steady state densi- 322 ties, though far enough away to avoid large-amplitude transient 323 cycles. The fact that allometric values of σ and ρ fall within 324 this relatively small window supports the possibility that a se- 325 lective mechanism has constrained the physiological conditions 326 driving observed starvation and recovery rates within popula-

332 nance. Nevertheless, our finding that allometrically-determined 380 tated subset of the population (identified by χ) where individu-
333 energetic rates place the system within this low probability of 381 als have a modified proportion of body fat $M' = M(1 + \chi)$
334 extinction region suggests that the NSM system provides gen- 382 where $\chi \in [-0.5, 0.5]$, thus altering rates of starvation, re-
335 eral insight to a phenomena that may both drive – and constrain 383 covery, and maintenance β . Although there is not an internal
336 – natural animal populations. 384 fixed point where both residents and invaders coexist (except
337 **Dynamic and energetic barriers on body size** 385 for the trivial state $\chi = 0$), we can assess invasibility as a func-
338 Metabolite transportation constraints are widely thought to 386 tion of organismal mass by determining which consumer steady
339 place strict boundaries on biological scaling [40, 41, 42], lead- 387 state is larger across values of modified body fat. We find that
340 ing to specific predictions on the minimum possible body size 388 for $1 \leq M < 10^6$ g, having additional body fat ($\chi > 0$) re-
341 for organisms [43]. In the opposite vein, a number of ener- 389 sults in a higher steady state density for the invader population
342 getic and evolutionary mechanisms have been explored to as- 390 ($H'^* + F'^* > H^* + F^*$), such that it has an intrinsic advantage
343 sess the costs and benefits of larger body masses, particularly 391 over the resident population. For $M > 10^6$, however, there is an
344 for mammals. The *fasting endurance hypothesis* contends that 392 increasing range of $\chi < 0$ such that leaner individuals have the
345 larger body size, being energetically more efficient per unit 393 advantage, and this is due to the changing covariance between
346 biomass, may buffer organisms against environmental fluctu- 394 energetic rates as a function of modified body fat.
347 ations in resource availability [44]. Over evolutionary time, ter-
348 restrial mammalian lineages show a significant trend towards 395 The observed switch in invasibility as a function of χ at
349 larger body size (known as Cope’s Rule) [45, 46, 47, 48], and it 396 $M_{\text{opt}} \approx 10^6$ thus serves as an attractor, where over evolu-
350 is thought that within-lineage drivers may instigate a selective 397 tionary time the NSM predicts organismal mass to increase if
351 force towards an optimal upper-bound of ca. 10^7 grams [45], the 398 $M < M_{\text{opt}}$ and decrease if $M > M_{\text{opt}}$. Moreover, M_{opt} , which
352 value of which may be due to higher extinction risks for large 399 is entirely determined by the population-level consequences of
353 taxa over longer timescales [46]. These evolutionary trends are 400 energetic constraints is within an order of magnitude as that
354 thought to be driven by a combination of climate and niche 401 observed in the North American mammalian fossil record [45]
355 availability [48], however the underpinning energetic costs and 402 and as that predicted from an evolutionary model of body size
356 benefits of larger body sizes, and how they influence dynamics 403 evolution [46]. Of course, the state of the environment in com-
357 over ecological timescales, has not been explored, and we con- 404 bination with the realized competitive landscape will determine
358 tend that the NSM provides a suitable framework to explore 405 whether specific body size classes are selected for or not [48],
359 this problem. 406 however the internal dynamic that we examine with the NSM
360 The NSM correctly predicts that species with smaller 407 may supply the fundamental momentum fueling the evolution
361 masses have larger steady state population densities, however 408 of larger body size among terrestrial mammals.
362 we observe that there is a sharp asymptote in both steady state 409 The energetics associated with somatic maintenance,
363 densities as well as σ/ρ at $M \approx 0.3$ grams (Fig. 6b). Observa- 410 growth, and reproduction are important elements that influ-
364 tion of the rates of starvation and recovery explain why: as mass 411 ence the dynamics of all populations [9]. The NSM is a mini-
365 decreases, the rate of starvation increases steadily, while the rate 412 mal and general model that incorporates the dynamics of star-
366 of recovery begins to decline precipitously. This exponential de- 413 vation that are expected to occur in resource limited environ-
367 cline in ρ occurs when body fat percentage is $1 - 1/(cM) \approx 2\%$, 414 ments. By incorporating allometric relationships between the
368 whereupon consumers have no eligible route out of starvation, 415 rates in the NSM, we find *i*) different organismal masses are
369 leading to extinction. Compellingly, this dynamic bound deter- 416 more or less prone to different population dynamic regimes,
370 mined by the rate of energetic recovery is close to the minimum 417 *ii*) allometrically-determined rates of starvation and recovery
371 observed mammalian body size of ca. 1.3–2.5 grams (Fig. 6b,c), 418 appear to minimize extinction risk, and *iii*) the dynamic conse-
372 a range that occurs as the recovery rate begins to decline ex- 419 quences of these rates may place additional barriers on the evo-
373 ponentially. In addition to barriers associated with metabolite 420 lution of minimum and maximum body size. We suggest that
374 transport constraints [43], we suggest that an additional limi- 421 the NSM offers a means by which the dynamic consequences
375 tation stems from the dynamics of starvation. 422 of energetic constraints can be assessed using macroscale inter-
376 Although there are upper bounds to the rate equations (e.g. 423 actions between and among species. Future efforts will involve
377 when percent body fat becomes unity), they are not biolog- 424 exploring the consequences of these dynamics in a spatially ex-
378 ically feasible and we do not discuss them further. Instead, 425 plicit framework, thus incorporating elements such as movement
379 we investigate population invasibility with respect to a mu- 426 costs and spatial heterogeneity, which may elucidate additional
427 tradeoffs associated with the dynamics of starvation.

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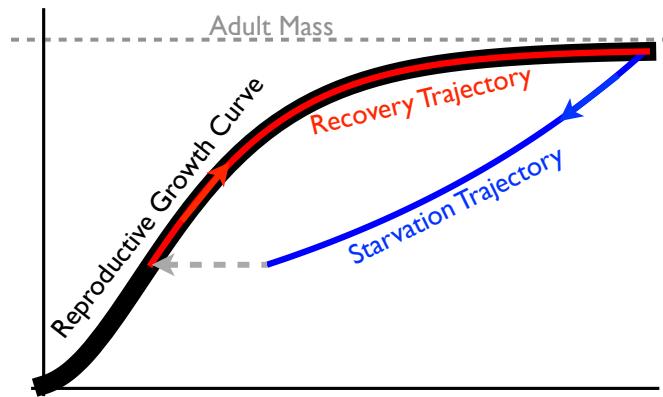


Fig. 1

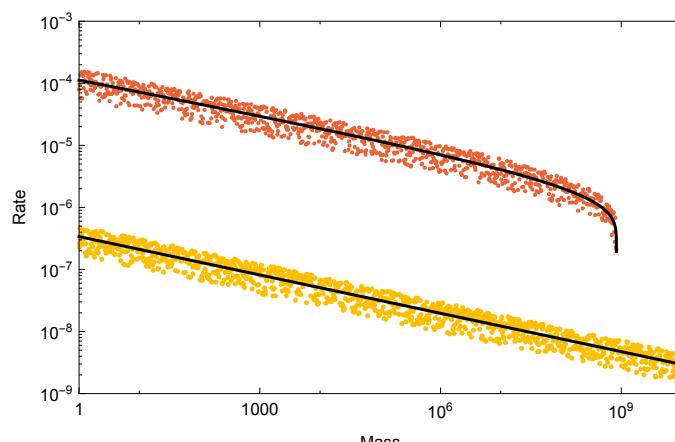


Fig. 2

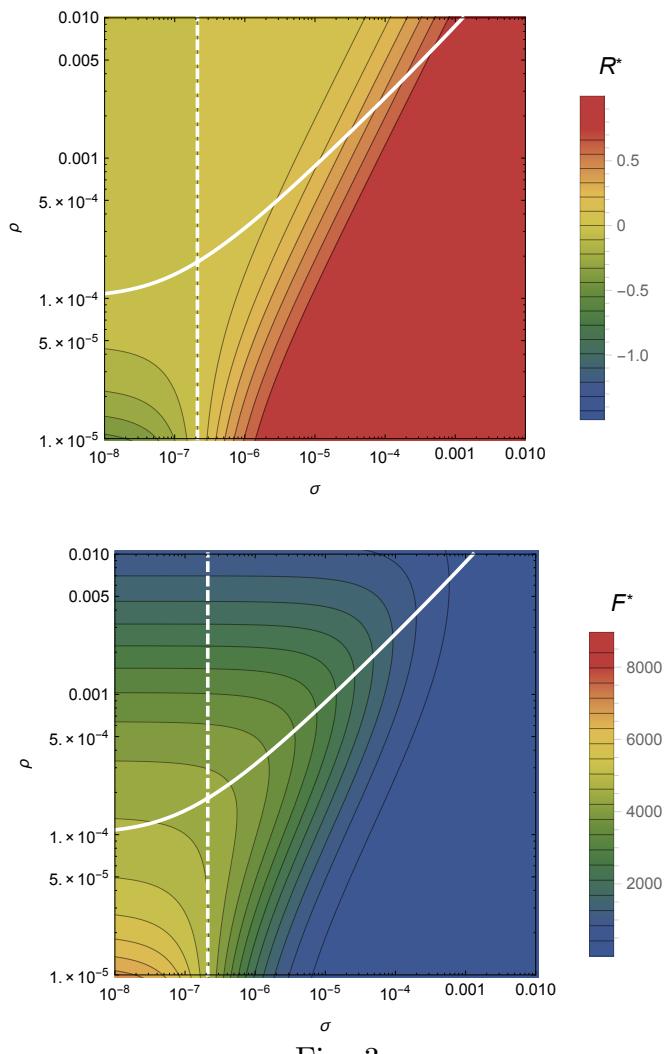


Fig. 3

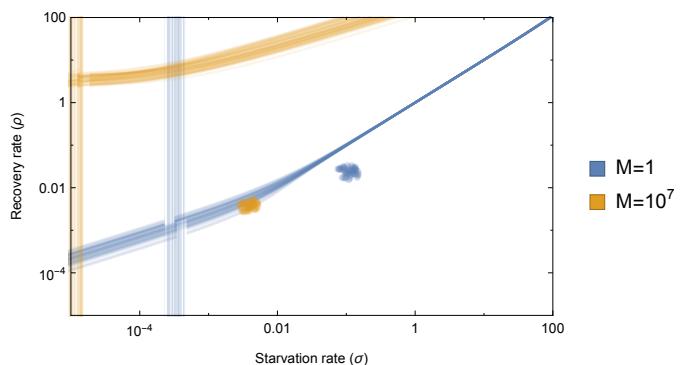


Fig. 4

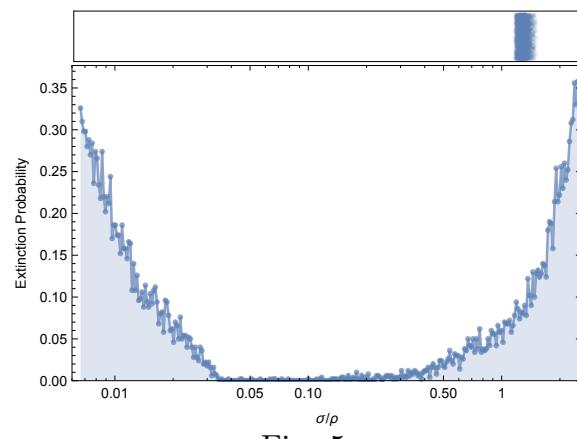


Fig. 5

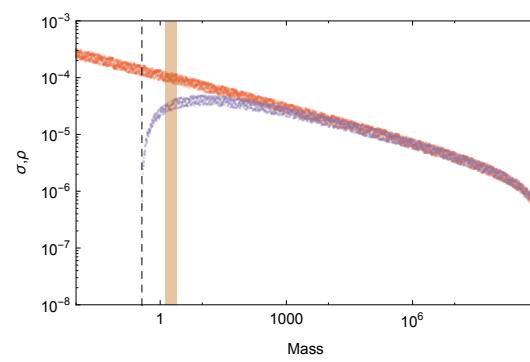
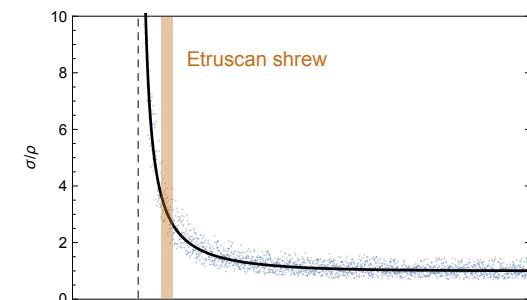
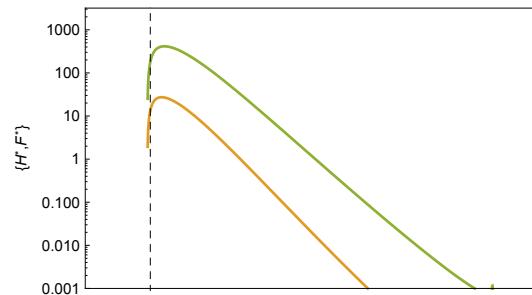


Fig. 6

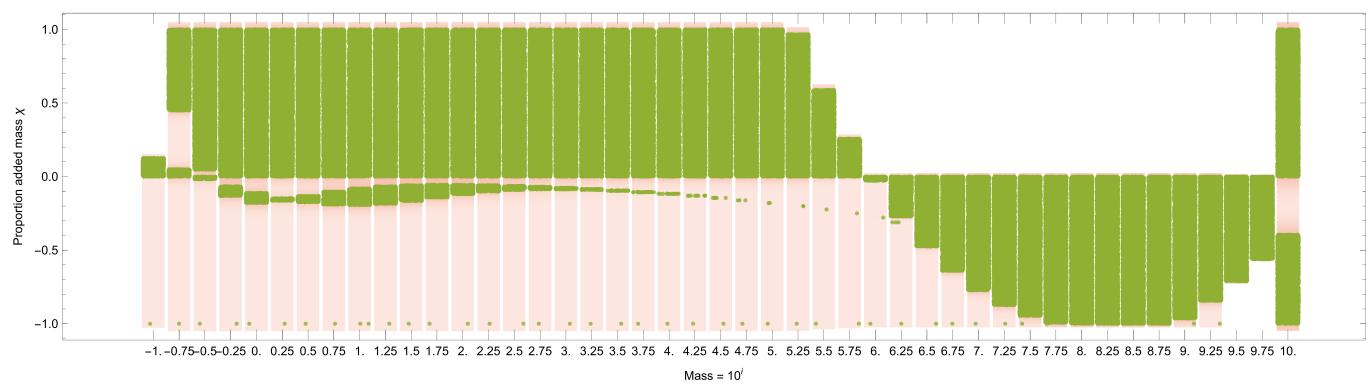


Fig. 7

Table 1: Parameter Values For Various Classes of Organisms

	Mammals	Unicellular karyotes	Eu- karyotes	Bacteria
η	3/4			1.70
E_m	10695 (J gram ⁻¹)			10695 (J gram ⁻¹)
E'_m	$\approx E_m$			$\approx E_m$
B_0	0.019 (W gram ^{-α})			1.96×10^{17}
B_m	0.025 (W gram ⁻¹)			0.025 (W gram ⁻¹)
a	1.78×10^{-6}			1.83×10^{13}
b	2.29×10^{-6}			2.29×10^{-6}
$\eta - 1$	-0.21			0.73
λ_0	3.39×10^{-7} (s ⁻¹ gram ^{1-η})			56493
γ	1.19			0.68
f_0	0.02			1.30×10^{-5}
ζ	1.01			
mm_0	0.32			