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# SURVIVAL OF THE FITTEST IN A GENERALIZED LOGISTIC MODEL

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In this paper we discuss the asymptotic behavior of a logistic model with distributed growth and mortality rates. In particular, we prove that the entire population becomes concentrated within the subpopulation with highest growth to mortality ratio, and converges to the equilibrium defined by this ratio. Finally, we present a numerical example illustrating the theoretical results.

## 1. Introduction

Modeling population dynamics often involves balancing the competing requirements of realism and simplicity. On the side of simplicity, we have the classical Kolmogorov models, which have been extensively studied for decades. Since such models treat all individuals as identical, they cannot be expected to provide an adequate representation of the dynamics of most biological populations, unless they are modified in such a way to allow for different individuals or subpopulations to have different growth or mortality rates. On the side of realism, we have individual based models, which often involve rather complex and computationally intensive simulations. In recent years, several researchers have focused on generalizing Kolmogorov population models, as well as Sinko–Streifer population models, to allow for rates to vary across individuals (see Ackleh,[1] Banks *et al.*,[4,6] Banks and Fitzpatrick,[5] and Fitzpatrick[10]). In this paper, we are interested in the asymptotic behavior of a generalization of the classical logistic population model, a generalization that allows for individuals or subpopulations to have different growth and mortality rates.

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The original model is given by:

$$\begin{cases} \dfrac{dX(t)}{dt} = X(t)[q_1 - q_2 X(t)]\,, \\ X(0) = X^0\,. \end{cases} \tag{1.1}$$

In (1.1), $X(t)$ denotes the total population at time $t$. The parameters $q_1$ and $q_2$ are the fixed growth and mortality rates, respectively. Note that these two parameters are meant to represent properties of all individuals in the population. In order to incorporate differences among individual growth and mortality, we must alter the model.

We begin by assuming that the population is divided into subpopulations having growth and mortality parameters $q = (q_1, q_2)$ lying in the set $Q = [a_1, b_1] \times [a_2, b_2]$, where $a_1$, $a_2$, $b_1$, $b_2 \in \mathbb{R}^+$. Note that the point $q^* = (b_1, a_2)$ gives the subpopulation with the highest growth to mortality ratio. This subpopulation will play an important role in the asymptotic behavior of our model. The model is constructed using subpopulation densities as state variables: we denote by $x(t, q)$ the density of individuals at time $t$ having parameter $q$. Hence, for any subset $\widehat{Q} \subset Q$, the part of the population having parameters $q \in \widehat{Q}$ is given by

$$\int_{\widehat{Q}} x(t, q)\, dq\,.$$

Following Ackleh[1] we assume that growth is subpopulation specific, while mortality is driven by interaction with the entire population. This leads to the following generalized logistic model, which is the topic of study in this paper:

$$\begin{cases} \dfrac{dx(t,q)}{dt} = x(t,q)[q_1 - q_2 X(t)]\,, \\ x(0,q) = x_0(q)\,, \end{cases} \tag{1.2}$$

where $X(t) = \int_Q x(t,q)\,dq$ is the total population at time $t \geq 0$. For more details on this approach of generalizing classical Kolmogorov population models we refer the reader to the papers by Ackleh[1] or Banks *et al.*[6] In the paper by Ackleh[1] the existence, uniqueness, and non-negativity of global solutions $x \in C^1([0,\infty); C(Q))$ were established for a broad class of community models, including (1.2); this was done using the theory of differential equations in abstract spaces discussed in Ladas and Lakshmikantham.[11]

Our paper is organized as follows. In Sec. 2, we determine the asymptotic behavior of solutions of system (1.2). There it is shown that for non-negative initial conditions $x_0(q) \in C(Q)$, $x_0(q^*) \neq 0$, the population density evolves in time so that the entire surviving population becomes concentrated (in the limit) at $q^*$. This is survival of the fittest, where the "fittest" are those from the subpopulation possessing the characteristic $q^*$ (that maximizes the growth to mortality ratio for the parameter space). In Sec. 3 we present numerical results to illustrate this evolution. Section 4 is devoted to conclusions and possible directions for future research.

## 2. Asymptotic Behavior of the Generalized Model

The basic idea behind the main result of this paper is that $x(t,q) \to c\delta_{q^*}(q)$ as $t \to \infty$, where $\delta_{q^*}$ denotes the Dirac delta function concentrated at $q^*$. The constant $c$ turns out to be the ratio $b_1/a_2$. In order to make the statement mathematically rigorous, we rely on the theory of weak convergence of probability measures. Thus, we begin by normalizing the density $x(t,q)$.

For any Borel subset $E$ of $Q$, define the set function $P_t$ via:

$$P_t(E) = \frac{\int_E x(t,q)\,dq}{\int_Q x(t,q)\,dq} = \frac{1}{X(t)} \int_E x(t,q)\,dq\,.$$

Then $P_t$ is a probability measure on $(Q, \mathcal{B})$, where $\mathcal{B}$ is the $\sigma$-field whose elements are the Borel subsets of the parameter space $Q$. Note that for each time $t$, we get a different probability measure $P_t$. We are concerned with the limiting behavior of $P_t$ as $t \to \infty$. This limit will be discussed in terms of weak convergence of probability measures. The pertinent results from that general theory we state next for convenience; a thorough discussion of this material can be found in Ash,[3] Billingsley,[7,8] and Ethier and Kurtz.[9]

Let $S$ be a complete separable metric space with metric $d$. Denote by $\mathcal{P}(S)$ the space of probability measures on the Borel subsets of $S$. For any closed set $F$ in $S$ and $\varepsilon > 0$, define

$$F_\varepsilon = \left\{ x \in S : \inf_{y \in F} d(x,y) < \varepsilon \right\}.$$

Clearly $F \subset F_\varepsilon$. Also, if $P_1$, $P_2 \in \mathcal{P}(S)$, put

$$\rho(P_1, P_2) = \inf\{\varepsilon > 0 : P_1[F] \le P_2[F_\varepsilon] + \varepsilon, \text{ for all closed } F \in S\}\,.$$

It is known that $\rho$ is a metric on $\mathcal{P}(S)$, and that $\mathcal{P}(S)$ is a complete metric space under $\rho$. Furthermore, if $S$ is compact, then $\mathcal{P}(S)$ is also compact. The following theorem characterizes the weak convergence of probability measures with respect to the metric $\rho$ (see, e.g. Ethier and Kurtz,[9] p. 108).

**Theorem 2.1.** *Let $(S,d)$ be a metric space that is both separable and complete. Let $P_n \subset \mathcal{P}(S)$, $P \in \mathcal{P}(S)$. Then, the following are equivalent*:

(a) $\rho(P_n, P) \to 0$, *as* $n \to \infty$;
(b) $\int_S f\,dP_n \to \int_S f\,dP$, *for all bounded, uniformly continuous, real-valued functions* $f$ *on* $S$;
(c) $P_n[D] \to P[D]$, *for all Borel sets* $D$ *with* $P[\partial D] = 0$.

Note that this theorem implies that convergence under the metric $\rho$ is equivalent to convergence in distribution. We stated above that the population density, i.e. the solution of (1.2), evolves in such a way as to make the entire population become concentrated at the characteristic $q^*$, as $t \to \infty$. We are now ready to state our goal rigorously: show that $\lim_{t\to\infty} P_t = \delta_{q^*}$, where the limit is taken in the metric $\rho$. By Theorem 2.1 this is equivalent to the following theorem.

**Theorem 2.2.** *For every continuous real-valued function $f$ defined on $Q$,*

$$\lim_{t\to\infty}\left|\int_Q f(q)\,dP_t - f(q^*)\right| = 0\,.$$

Our proof makes use of two lemmas, the first of which concerns the boundedness and strict positivity of the total population.

**Lemma 2.3.** *If $x(t,q)$ is a solution of system* (1.2) *with non-negative initial conditions $x(0,q)\in C(Q)$ such that $x(0,q^*)>0$, then the total population is bounded and strictly positive, i.e. there exist $m$, $M>0$ such that $\forall\, t\ge 0$, $m\le X(t)\le M$.*

**Proof.** Note that $x(t,q)$ and $\frac{d}{dt}x(t,q)$ are continuous in $t$ and $q$. So we obtain

$$\frac{d}{dt}X(t) = \int_Q x(t,q)[q_1 - q_2X(t)]\,dq\,. \tag{2.1}$$

Suppose $X(0) > 2b_1/a_2$, where $b_1$ and $a_2$ are the growth and mortality parameters for $q^*$. Since $X$ is continuous, there exists a time $T>0$ such that $X(t) > 2b_1/a_2$, $\forall\, t\in[0,T)$. Then, for such $t$,

$$q_1 - q_2X(t) < q_1 - q_2\left(\frac{2b_1}{a_2}\right) \le q_1 - 2b_1 \le -b_1\,.$$

Using this, together with (2.1) and the non-negativity of $x(t,q)$, we obtain

$$\frac{d}{dt}X(t) \le -b_1\int_Q x(t,q)\,dq = -b_1X(t)\,. \tag{2.2}$$

Consequently $X(t)\le X(0)\exp(-b_1t)$, for all $t\in[0,T)$. If $T=\infty$, then clearly $X(0)$ is an upper bound $\forall\, t\ge 0$. Suppose $T$ is finite. By continuity, $X(T)=2b_1/a_2$, and it is clear that $X$ will never again exceed this value. In fact, if $X$ exceeds $2b_1/a_2$ at some time beyond $T$, then the continuity of $X$ implies the existence of times $\tau_1\ge T$ and $\tau_2>\tau_1$ such that $X(\tau_1)=2b_1/a_2$, and $X(t)>2b_1/a_2$, $\forall\, t\in(\tau_1,\tau_2]$. The mean value theorem then assures the existence of at least one time $t'\in(\tau_1,\tau_2)$ such that $\frac{dX(t)}{dt}\big|_{t=t'} > 0$, contrary to prior argument. On the other hand, if $0 < X(0)\le 2b_1/a_2$, then arguing as above one can show that $2b_1/a_2$ is an upper bound for $X(t)$, $\forall\, t\ge 0$. Hence, $M=\max\{2b_1/a_2, X(0)\}$ is an upper bound for $X(t)$, $\forall\, t\ge 0$.

To obtain a strictly positive lower bound, suppose that $0 < X(0) < a_1/(2b_2)$. An argument similar to the one above, but using the inequalities

$$q_1 - q_2X(t) > q_1 - q_2\left(\frac{a_1}{2b_2}\right) \ge q_1 - \frac{a_1}{2} \ge \frac{a_1}{2}\,,\qquad t\in[0,T')$$

and

$$\frac{d}{dt}X(t) \ge \frac{a_1}{2}\int_Q x(t,q)\,dq = \frac{a_1}{2}X(t)\,,\quad t\in[0,T')\,,$$

for some $T' > 0$, shows that $X(t) \geq X(0)$, $\forall\, t \geq 0$. Also, if $X(0) \geq a_1/(2b_2)$, then $X(t) \geq a_1/(2b_2)$, $\forall\, t \geq 0$. Then $m = \min\{a_1/(2b_2), X(0)\}$ is a positive lower bound. ☐

We next prove that the population over all the parameter spaces $Q$, except for an arbitrarily small ball centered at $q^*$, goes to zero as $t \to \infty$. In the proof we assume, without loss of generality, that $q_1 \geq 1$. If this is not the case, then choose a constant $E$ such that $q_1/E \geq 1$ and rescale the model (1.2) in the following manner:

$$\begin{cases} \dfrac{dx(t,q)}{dt} = Ex(t,q)[\bar{q}_1 - \bar{q}_2 X(t)]\,, \\ x(0,q) = x_0(q)\,, \end{cases} \tag{2.3}$$

with $\bar{q}_i = q_i/E$, $i = 1, 2$. Then one can easily verify that the results of this section hold true for the rescaled system (2.3). Using the assumption that $q_1 \geq 1$, together with Young's inequality, we obtain the boundedness of $\int_Q x^{1/q_1}(t,q)\,dq$ from the boundedness of $X(t)$.

**Lemma 2.4.** *Let* $0 < \delta < \min\{b_1 - a_1, b_2 - a_2\}$. *Let* $B_\delta$ *be the intersection of* $Q$ *with the ball of radius* $\delta$ *centered at* $q^*$. *Then* $\int_{Q\setminus B_\delta} x(t,q)\,dq \to 0$, *as* $t \to \infty$.

**Proof.** Once $\delta > 0$ is given, distinct lines L1 and L2 can be chosen to separate $Q$ into the regions $A$, $B$ and $C$, as shown in Fig. 1. Note that $Q\setminus B_\delta \subset A$. Since L1 passes through the origin, every point $q$ on L1 has the same ratio $q_1/q_2$. This property holds for L2 as well. Note that for any point $p = (p_1, p_2) \in A$ and any point $q = (q_1, q_2) \in C$, we have $p_2/p_1 > q_2/q_1$.

Let $r(t) = \frac{x^{1/p_1}(t,p)}{x^{1/q_1}(t,q)}$, where $p$ is any fixed point in $A$ and $q$ is any point in region $C$. Then

$$\begin{aligned} \frac{d}{dt} r(t) &= \frac{x^{1/q_1}(t,q)}{x^{2/q_1}(t,q)} \left( \frac{1}{p_1} x^{1/p_1 - 1}(t,p) x(t,p)(p_1 - p_2 X(t)) \right) \\ &\quad - \frac{x^{1/p_1}(t,p)}{x^{2/q_1}(t,q)} \left( \frac{1}{q_1} x^{1/q_1 - 1}(t,q) x(t,q)(q_1 - q_2 X(t)) \right) \\ &= \left( \frac{q_2}{q_1} - \frac{p_2}{p_1} \right) X(t) r(t)\,. \end{aligned}$$

Since $q \in C$ and $p \in A$, the quantity $(q_2/q_1 - p_2/p_1)$ is negative. So we have a first order ordinary differential equation in $r(t)$ whose solution satisfies:

$$r(t) \leq K \exp\left( -\lambda \int_0^t X(\xi)\,d\xi \right)\,,$$

where

$$K = \sup_{p\in A, q\in C} \frac{x^{1/p_1}(0,p)}{x^{1/q_1}(0,q)} \quad \text{and} \quad -\lambda = \sup_{p\in A, q\in C} \left( \frac{q_2}{q_1} - \frac{p_2}{p_1} \right)\,.$$

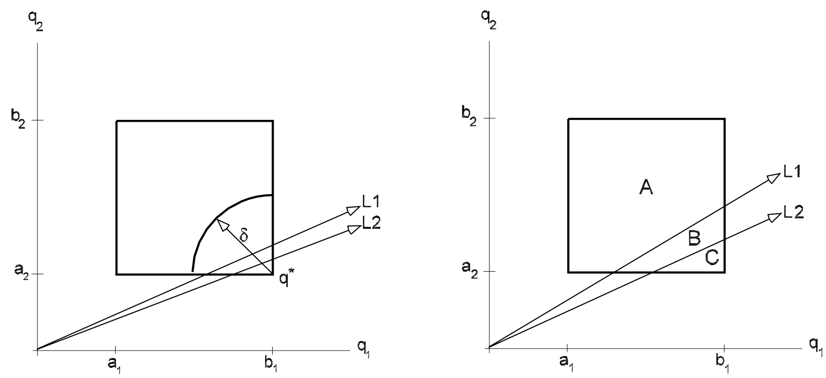


Fig. 1. Regions for Lemma 2.4.

If $m > 0$ is the lower bound for $X(t)$ established in Lemma 2.3, then $r(t) \leq K\exp(-\lambda mt)$. That is,

$$x^{1/p_1}(t,p) \leq K\exp(-\lambda mt)x^{1/q_1}(t,q)\,.$$

Since $x(t,q)$ is non-negative, for fixed $p \in A$ we have:

$$\int_C x^{1/p_1}(t,p)\,dq = x^{1/p_1}(t,p)\mu(C) \leq Ke^{-\lambda mt}\int_C x^{1/q_1}(t,q)\,dq\,,$$

where $\mu$ is Lebesgue measure on $\mathbb{R}^2$. Since $\mu(C) > 0$, we have

$$x^{1/p_1}(t,p) \leq \frac{Ke^{-\lambda mt}}{\mu(C)}\int_C x^{1/q_1}(t,q)\,dq\,.$$

The integral on the right-hand side of the inequality is bounded. Since the right-hand side is independent of $p$, we see that $x^{1/p_1}(t,p) \to 0$ uniformly on $A$ as $t \to \infty$. Since $p_1$ is an element of a bounded interval, we also have $x(t,p) \to 0$ uniformly on $A$ as $t \to \infty$. So

$$\int_{Q\setminus B_\delta} x(t,q)\,dq \leq \int_A x(t,q)\,dq \to 0 \quad \text{as} \quad t \to \infty\,. \qquad \square$$

Now that we have established the requisite lemmas, we prove the main theorem.

**Proof of Theorem 2.2.** Let $\varepsilon > 0$. Then

$$\begin{aligned}&\left|\frac{\int_Q f(q)x(t,q)\,dq}{X(t)} - f(q^*)\right|\\ &\quad\leq \frac{1}{X(t)}\left\{\left|\int_{B_\delta}(f(q)-f(q^*))x(t,q)\,dq\right|\right.\\ &\qquad\left.+\left|\int_{Q\setminus B_\delta} f(q)x(t,q)\,dq\right| + \left|f(q^*)\left(\int_{B_\delta} x(t,q)\,dq - X(t)\right)\right|\right\}\end{aligned}$$

$$\leq \frac{1}{m}\left\{ \left|\int_{B_\delta} (f(q) - f(q^*))x(t,q)\,dq\right| \right.$$
$$\left. + \left|\int_{Q\setminus B_\delta} f(q)x(t,q)\,dq\right| + \left|f(q^*)\left(\int_{B_\delta} x(t,q)\,dq - X(t)\right)\right| \right\}$$
$$= \mathrm{I} + \mathrm{II} + \mathrm{III}\,,$$

where $m$ is the lower bound for the total population established in Lemma 2.3. Let $M$ be the upper bound for the total population established in Lemma 2.3. By continuity of $f$, we may choose $\delta$ small enough so that $|f(q) - f(q^*)| < \varepsilon m/3M$, $\forall\, q \in B_\delta$. We have

$$\mathrm{I} = \frac{1}{m}\left|\int_{B_\delta} (f(q) - f(q^*))x(t,q)\,dq\right| \leq \frac{\varepsilon}{3M}\int_{B_\delta} x(t,q)\,dq \leq \frac{\varepsilon}{3M}\int_Q x(t,q)\,dq < \frac{\varepsilon}{3}\,.$$

Let $U = \sup_{q\in Q}|f(q)|$. Using Lemma 2.4, choose $T$ large enough such that

$$\int_{Q\setminus B_\delta} x(t,q)\,dq < \frac{\varepsilon m}{3U}\,.$$

Then we have that, $\forall\, t > T$,

$$\mathrm{II} = \frac{1}{m}\left|\int_{Q\setminus B_\delta} f(q)x(t,q)\,dq\right| \leq \frac{U}{m}\int_{Q\setminus B_\delta} x(t,q)\,dq < \frac{\varepsilon}{3}\,.$$

Similarly, $\forall\, t > T$,

$$\mathrm{III} = \frac{1}{m}\left|f(q^*)\left(\int_{B_\delta} x(t,q)\,dq - X(t)\right)\right| = \frac{|f(q^*)|}{m}\int_{Q\setminus B_\delta} x(t,q)\,dq$$
$$\leq \frac{U}{m}\int_{Q\setminus B_\delta} x(t,q)\,dq < \frac{\varepsilon}{3}\,.$$

Combining these results, we have that given $f \in C(Q)$ and $\varepsilon > 0$, there exists finite $T$ such that $\left|\frac{\int_Q f(q)x(t,q)\,dq}{X(t)} - f(q^*)\right| < \varepsilon$, $\forall\, t > T$, and the theorem is proved. □

At this point we sharpen our results. Lemma 2.3 says the total population is both strictly positive and bounded, while Lemma 2.4 says the part of the population located anywhere on $Q$, except for a small ball containing the point $q^* = (b_1, a_2)$, tends to zero as $t \to \infty$. Using these facts, we show that the total population $X(t)$ tends to a limit as $t \to \infty$.

**Lemma 2.5.** *Let* $\varepsilon > 0$ *be given. Then there exists* $T > 0$ *such that* $\forall\, t > T$, $|X(t) - b_1/a_2| < \varepsilon$.

**Proof.** Let $\eta > 0$ be such that $0 < \eta/a_2 < \varepsilon$. Suppose that for some time $\tau$ we have $X(\tau) > (b_1 + \eta)/a_2$. By the continuity of $X$, there exists $T_1 > 0$ such that $X(t) > (b_1 + \eta)/a_2$, $\forall\, t \in [\tau, T_1)$. Then, for such $t$,

$$q_1 - q_2 X(t) < q_1 - q_2 \left(\frac{b_1 + \eta}{a_2}\right) \le -\eta\,.$$

Using this inequality, together with (2.1), we obtain

$$\frac{d}{dt}X(t) = \int_Q x(t,q)[q_1 - q_2 X(t)]\,dq \le -\eta \int_Q x(t,q)\,dq = -\eta X(t)\,.$$

Consequently $X(t) \le g(t) = X(\tau)\exp(-\eta(t-\tau))$, for all $t \in [\tau, T_1)$. If $X(\tau) \le b_1/a_2 + \varepsilon$, then $X(t)$ is dominated on $[\tau, T_1)$ by $g(t)$ and so never exceeds $b_1/a_2 + \varepsilon$, $\forall\, t \in [\tau, T_1)$. If $X(\tau) > b_1/a_2 + \varepsilon$, then $(b_1 + \eta)/a_2 < X(t) < b_1/a_2 + \varepsilon$, when $-\frac{1}{\eta}\ln(\frac{b_1 + a_2\varepsilon}{a_2 X(\tau)}) + \tau < t < T_1$. If $T_1 = \infty$, we are done. If $T_1$ is finite, then $X(T_1) = (b_1 + \eta)/a_2$ by continuity of $X(t)$. A mean value theorem argument as in the proof of Lemma 2.3 assures that $X$ never again exceeds $X(T_1)$. Therefore there exists a finite time $\tau'$ such that $X(t) < b_1/a_2 + \varepsilon$, $\forall\, t > \tau'$.

Let $M$ and $m$ be the upper and lower bounds on the total population established in Lemma 2.3. By Lemmas 2.3 and 2.4, we may choose a time $T_2$ large enough so that $\forall\, t > T_2$,

$$\frac{1}{2}\int_{B_\delta} x(t,q)\,dq > \frac{m}{4}\,, \tag{2.4}$$

and

$$b_2 M \int_{Q\setminus B_\delta} x(t,q)\,dq < \frac{\eta m}{8}\,. \tag{2.5}$$

Suppose that for some time $\tau > T_2$ we have $X(\tau) < (b_1 - \eta)/a_2$. By the continuity of $X$, there exists $T_3 > \tau$ such that $X(t) < (b_1 - \eta)/a_2$, $\forall\, t \in [\tau, T_3)$. Choose $\delta > 0$ such that $\eta/(2a_2) > b_1/a_2 - q_1/q_2$, for all $q = (q_1, q_2) \in B_\delta$. Now

$$\frac{d}{dt}X(t) \ge a_1 \int_{Q\setminus B_\delta} x(t,q)\,dq - b_2 M \int_{Q\setminus B_\delta} x(t,q)\,dq + \int_{B_\delta} x(t,q)[q_1 - q_2 X(t)]\,dq \tag{2.6}$$

holds for any time $t \ge 0$. With $\delta$ as specified above, and for $t \in [\tau, T_3)$, we obtain

$$\begin{aligned}
\int_{B_\delta} x(t,q)[q_1 - q_2 X(t)]\,dq &> \int_{B_\delta} x(t,q)\left[q_1 - q_2\left(\frac{b_1 - \eta}{a_2}\right)\right]dq \\
&= \int_{B_\delta} x(t,q) q_2 \left[\frac{q_1}{q_2} - \left(\frac{b_1 - \eta}{a_2}\right)\right]dq \\
&= \int_{B_\delta} x(t,q) q_2 \left[\frac{\eta}{a_2} - \left(\frac{b_1}{a_2} - \frac{q_1}{q_2}\right)\right]dq \\
&> \int_{B_\delta} x(t,q) q_2 \left[\frac{\eta}{a_2} - \frac{\eta}{2a_2}\right]dq \\
&= \frac{\eta}{2}\int_{B_\delta} x(t,q)\frac{q_2}{a_2}\,dq \ge \frac{\eta}{2}\int_{B_\delta} x(t,q)\,dq\,.
\end{aligned} \tag{2.7}$$

Using (2.4)–(2.7), we conclude that $\frac{d}{dt}X(t) \geq \frac{\eta m}{8} > 0$, $\forall\, t \in [\tau, T_3)$. Consequently, $X(t) \geq X(\tau) + \frac{\eta m}{8}(t-\tau)$, $\forall\, t \in [\tau, T_3)$. Arguing in a fashion similar to the first case, we obtain the existence of a finite time $\tau''$ such that $X(t) > b_1/a_2 - \varepsilon$ for all $t > \tau''$.

In summary: Let $\varepsilon > 0$ be given. Then choose $\tau'$ and $\tau''$ as shown above, and let $T = \max\{\tau', \tau''\}$. Then $\forall\, t > T$, we have $|X(t) - b_1/a_2| < \varepsilon$, as claimed. □

Since, by Lemma 2.5, the total population tends to a limit, we have the following corollary of Theorem 2.2.

**Corollary 2.6.** *For every continuous real-valued function $f$ defined on $Q$,*

$$\lim_{t\to\infty} \left| \int_Q f(q)x(t,q)\,dq - \frac{b_1}{a_2} f(q^*) \right| = 0\,.$$

## 3. Numerical Results

To illustrate the behavior of the model via numerical simulation, we consider only a finite number of characteristics. We begin by choosing a partition $V$ of the parameter space $Q$. Let $V = V_1 \times V_2$, where

$$V_1 : a_1 = q_1^0 < q_1^1 < \cdots < q_1^{n_1} = b_1\,,$$
$$V_2 : a_2 = q_2^0 < q_2^1 < \cdots < q_2^{n_2} = b_2\,.$$

Let $N = n_1 \cdot n_2$. Define $\{Q^j\}$, $j = 1, \ldots, N$, to be the family of subrectangles of $Q$ resulting from the above defined partition, and assume that $|V| \to 0$ as $N \to \infty$, where $|V|$ is defined to be the largest edge length of all the subrectangles $Q^j$, i.e. $|V| = \max_k\{\max_{j=1}^N |q_k^j - q_k^{j-1}|\}$. Also, define $q^j = (q_1^j, q_2^j)$ to be the midpoint of the rectangle $Q^j$, $j = 1, \ldots, N$.

With these specifications we approximate the continuous model (1.2) by the following system of ordinary differential equations:

$$\begin{cases} \dfrac{dz^j(t)}{dt} = z^j(t)\left(q_1^j - q_2^j \displaystyle\sum_{i=1}^N \mu(Q^i) z^i(t)\right), \\ z^j(0) = \dfrac{1}{\mu(Q^j)} \displaystyle\int_{Q^j} x_0(q)\,dq\,. \end{cases} \tag{3.1}$$

Note that the variable $z^j$ has units that match the units of the continuous model solution. The existence, uniqueness, and non-negativity of global solutions of the discrete model (3.1) can be established using standard techniques for systems of ordinary differential equations.

Consider the family of simple functions defined by

$$U^N(t,q) = \sum_{j=1}^{N} z^j(t)\chi_{Q^j}(q)\,.$$

Using techniques as in Ackleh[1] the following convergence result can be established.

**Theorem 3.1.** *Let* $x_0(q) \in C(Q)$ *and* $T > 0$. *Then* $\sup_{q\in Q} |U^N(t,q) - x(t,q)| \to 0$, *as* $N \to \infty$, *uniformly on* $[0,T]$.

For a specific example, choose the parameter space $Q$ to be $[1,2] \times [1,2]$, and divide it into 100 evenly sized and spaced subrectangles $Q^j$, $j = 1,\ldots,100$. Let $Q^1$ be the subrectangle in the upper left corner of the parameter space $Q$. The subrectangle $Q^2$ lies immediately below $Q^1$, $Q^3$ below $Q^2$, etc. Once $Q^{10}$ is reached at the lower left corner of $Q$, move one step to the right and fill in the next column of subrectangles, with $Q^{11}$ at the top and $Q^{20}$ at the bottom. Continuing in this fashion, cover the parameter space $Q$ with the subrectangles, ending with $Q^{100}$ in the lower right corner. As in the preceding discussion, choose the points $q^j$, $j = 1,\ldots,100$, to be the midpoints of the subrectangles $Q^j$.

For this discretization, we numerically solve system (3.1) with $N = 100$ and $0 \le t \le 80$. The initial population density over the parameter space is $z^j(0) = 100e^{-4(q_1^j-1.5)^2}e^{-4(q_2^j-1.5)^2}$, $j = 1,\ldots,100$. Solving (3.1) with these initial conditions, we obtain the results indicated in Figs. 2–5.

In Fig. 3, where $t = 0.03$, we see that the initial conditions are quickly being flattened out. In Fig. 4, no visible traces of the initial conditions remain, and the density is beginning to concentrate near $q^{100}$. By the time $t = 80$, the density is concentrated at $q^{100}$, as shown in Fig. 5.

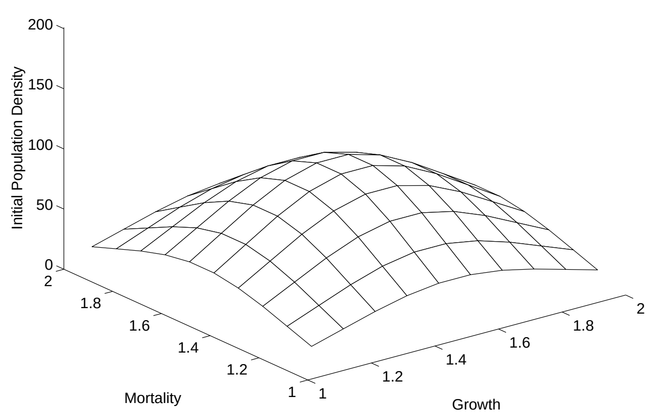


Fig. 2. Initial conditions.

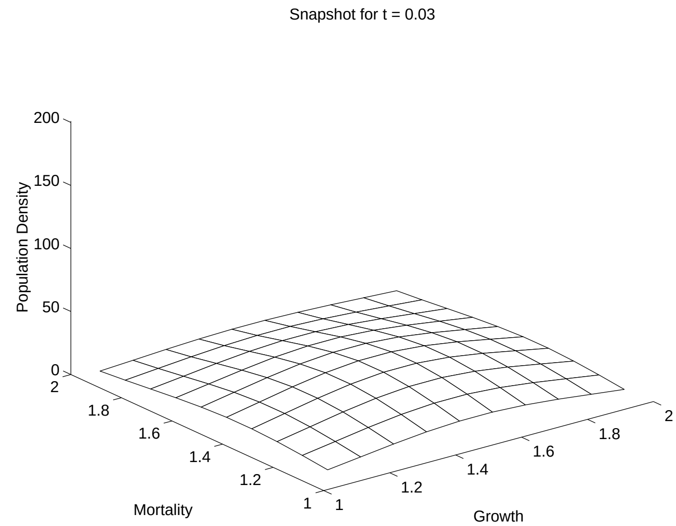


Fig. 3. Short time solution.

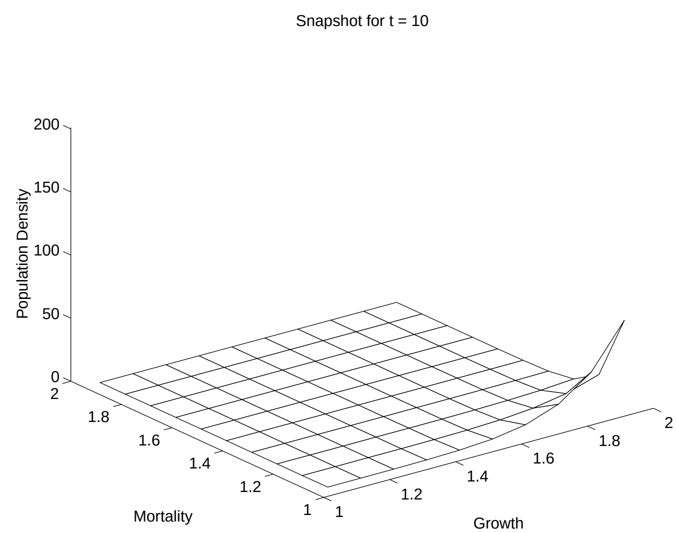


Fig. 4. Middle time solution.

In Sec. 2, we proved that the limiting value of the total population for the generalized logistic model is the maximum value of the growth to mortality ratio for the points in the parameter space $Q$. In the numerical simulation, this maximum occurs at $q^{100}$. For our discretization, $q_1^{100} = 1.95$ and $q_2^{100} = 1.05$, so the ratio is $1.95/1.05 = 1.8571$. This matches what we get when we multiply the equilibrium density for $z^{100}$, which is 185.71, by the measure of $Q^{100}$, which is 0.01.

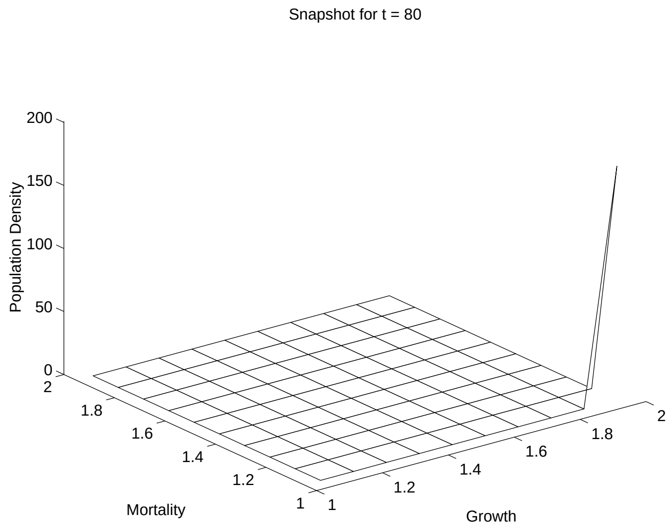


Fig. 5. Long time solution.

## 4. Conclusions

We have shown that survival of the fittest, as defined in the Introduction, holds for the generalized logistic model (1.2). Not only does the population density $x(t, q)$ become concentrated at the point $q^*$, it converges *uniformly* to zero on any subset of the parameter space that excludes a small ball centered at $q^*$. We believe that the main underlying assumption in the model (1.2) that leads to such dynamics is that growth is subpopulation specific. That is, each subpopulation with parameter $q$ is closed under reproduction. Our current research is focused on modifying this assumption and allowing for individuals that belong to subpopulations with characteristics $\bar{q} \in Q$ to reproduce individuals with characteristics $q$. Theoretical and computational results for a special case of this modification suggest that several subpopulations survive, not only the fittest (see Ackleh *et al.*[2]). In addition, the assumption that growth is subpopulation specific was used in the development of generalized Kolmogorov models in Ackleh.[1] We plan to investigate the conditions on the interaction functions and the parameters that lead to survival of the fittest in the general Kolmogorov population models.

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