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## ON THE CONVERGENCE OF THE ESCALATOR BOXCAR TRAIN\*

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**Abstract.** The Escalator Boxcar Train (EBT) is a numerical method that is widely used in theoretical biology to investigate the dynamics of physiologically structured population models, i.e., models in which individuals differ by size or other physiological characteristics. The method was developed more than two decades ago, but has so far resisted attempts to give a formal proof of convergence. Using a modern framework of measure-valued solutions, we investigate the EBT method and show that the sequence of approximating solution measures generated by the EBT method converges weakly to the true solution measure under weak conditions on the growth rate, birth rate, and mortality rate. In rigorously establishing the convergence of the EBT method, our results pave the way for wider acceptance of the EBT method beyond theoretical biology and constitutes an important step towards integration with established numerical schemes.

**Key words.** escalator boxcar train, convergence, physiologically structured population models, measure-valued solutions, transport equation, particle methods

**AMS subject classifications.** 65M12, 28A33, 92B05

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**1. Introduction.** The population dynamics of ecological and biological systems are often described by an ordinary differential equation of the form

$$\frac{1}{N} \frac{dN}{dt} = \beta(N) - \mu(N),$$

where  $N = N(t)$  is the total population size at time  $t$ ,  $\beta(N)$  is the birth rate, and  $\mu(N)$  is the mortality rate, both of which depends on the population size. The key assumption in this type of model is that every individual in the population is identical. This is clearly unreasonable in many situations, including cases where the gap between birth size and reproductive size is important. A more accurate description of the population dynamics can be given by physiologically structured population models (see, e.g., [25]). In these models, the birth rates, death rates, and growth rates of individuals depend on their physiological state  $x \in \Omega$ , where  $\Omega$  is the set of admissible states. In general, these states can represent any aspects of individual physiology such as age, size, mass, height, or girth. For the purpose of this paper, we will work with a one-dimensional state space that we think of as representing individual size, but other interpretations are possible and, as we note in the concluding discussion, we expect that our results can easily be extended to higher-dimensional state manifolds.

In order to specify a physiologically structured population model, we need explicit representations for the mortality, growth, and fecundity rates of individuals as well as the initial population structure. We assume that these rates are, respectively, on the forms  $\mu(x, E_t)$ ,  $g(x, E_t)$ , and  $\beta(x, E_t)$ , where  $x$  is the size (or, more generally,

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the state) of the individual and  $E_t$  is the environment that individuals experiences at time  $t$ . The environment is a key factor in the formulation of physiologically structured population models and can, for example, represent the total amount of nutrient available at time  $t$  or the size-specific predation rate; see, e.g., [25, 8]. While the environment is often low-dimensional, it could potentially be infinite-dimensional as would, for example, be the case for the shading profile in a forest. Finally, we assume that all new individuals have the same birth size  $x_b$ . With these assumptions, one can show (see, e.g., [8]) that the density  $u(x, t)$  of individuals of state  $x$  at time  $t$  is given by the first order, nonlinear, nonlocal hyperbolic partial differential equations with nonlocal boundary condition

$$(1.1a) \quad \frac{\partial}{\partial t} u(x, t) + \frac{\partial}{\partial x} (g(x, E_t) u(x, t)) = -\mu(x, E_t) u(x, t),$$

$$(1.1b) \quad g(x_b, E_t) u(x_b, t) = \int_{x_b}^{\infty} \beta(\xi, E_t) u(\xi, t) d\xi,$$

$$(1.1c) \quad u(x, 0) = u_0(x),$$

in which we assume that  $x_b \leq x < \infty$  and  $t \geq 0$ . Note that the nonlocality arises not only from the boundary condition, but also from the dependence of the coefficients on the experienced environment  $E_t$ . We assume  $E_t = u(\cdot, t)$ , which makes the equation nonlinear and implies that the growth rate, birth rate, and mortality rate at time  $t$  are all dependent on the solution  $u(\cdot, t)$  at that very instant of time. The nonlocal dependence on the solution in both the equation and the boundary condition complicates the mathematical analysis of physiologically structured population models, but major advances in the theory of structured population models have nevertheless been made over the last two decades [15, 13, 10, 12, 11, 14, 18].

The first numerical method designed specifically for solving physiologically structured population models was the inventively named Escalator Boxcar Train (EBT) [7]. Rather than approximating the solution directly, it approximates the measure induced by the solution. This technique has been used for several decades in computational physics and forms the basis for a class of numerical schemes known as particle methods (see, e.g., [6, 21, 24, 27, 28]), though there is every reason to believe that the EBT method was invented independently. The EBT method differs from traditional particle methods in that newborn individuals need to be introduced recurrently as new particles, in a process known as internalization (see section 2). The accuracy of the numerical approximation thus depends on both a good approximation of the initial data and on sufficiently frequent internalizations.

The EBT method is commonly used in theoretical biology, with representative studies including [3, 17, 26, 29]. A likely reason for its widespread use in theoretical biology is that the components of the numerical scheme can be given a biological interpretation: the state-space is partitioned into initial cohorts and, for the  $i$ th cohort, the EBT method tracks its size  $N_i(t)$  and the location of its center of mass  $X_i(t)$ . The solution measure  $d\zeta_t := u(t, x) dx$  is then approximated by

$$(1.2) \quad d\zeta_t \approx d\zeta_t^N \equiv \sum_{i=B}^N N_i(t) \delta_{X_i(t)},$$

where  $\delta_x$  is the Dirac measure concentrated at  $x$ . The dynamics of the functions  $N_i$  and  $X_i$  will be defined in section 2. The boundary cohort corresponding to  $i = B$

is treated differentially from the other cohorts to account for newborn individuals. In the original formulation [7], this includes terms correcting for changes in the average mass arising from the inflow of newborn individuals. For completeness, we consider the original definition of the boundary cohort in section 4.

The convergence of the EBT method has remained an open question since the method was first introduced in 1988. The most successful analysis was performed by de Roos and Metz [9] in 1991. They studied how well the EBT method approximates integrals of the form  $\int_{\Omega} \psi(x)u(x, t) dx$  for smooth functions  $\psi$ , assuming that cohorts are not internalized. The result does not assert the *convergence* of the EBT method but rather, in the language used by de Roos and Metz, that the EBT method *consistently* approximates integrals of the solution to (1.1). One reason for the lack of progress is that the usual analytical techniques for analyzing finite element and finite difference schemes are not immediately applicable to the measure-valued case. Furthermore, the nonconservative nature of the underlying problem gives rise to fundamental difficulties when one tries to apply classical techniques from the literature on particle methods. First, the particle approximation (1.2) is not a solution to problem (1.1). Errors will accumulate due to the birth of new individuals, as described by the integral boundary condition, (1.1b). To keep these errors small, the EBT method requires the frequent internalization (addition) of new particles. Estimates of the accumulated errors must, therefore, be derived in terms of both the approximation of the initial data and the frequency of internalizations. A further difficulty arises from the nonlinear transformation that is used for internalizations, which we consider in section 4. Second, it is not generally possible to follow a characteristic curve of (1.1a) back to the initial data at time  $t = 0$ . Instead, one typically arrives at the boundary,  $x = x_b$ , at which the accuracy of the boundary value is difficult to assess as a consequence of the nonlocal dependence in the boundary condition, (1.1b). Thus, it is difficult to apply any analytical technique that depends on following characteristic curves back to the initial data.

The aim of this paper is to rigorously prove the convergence of the EBT method. We show that the EBT method converges under far weaker conditions on the growth, death, and birth functions than the conditions assumed by de Roos and Metz [9]. Our arguments build on theoretical developments by Gwiazda, Lorenz, and Marciniak-Czochra [18], specifically on their rigorous definition of measure-valued solutions of physiologically structured population models. In the following section, we describe the EBT method in full detail, define weak convergence of measures, and define weak solutions to the physiologically structured population model (1.1). Readers who are familiar with particle methods will recognize the main elements of the EBT method, but might still want to pay attention to the process of internalizations. In section 3 we prove the convergence of the EBT method with dynamics of the boundary cohort as introduced in this paper. Our convergence result is then extended to the original definition of the boundary cohort in section 4. We conclude by placing our results into context and by highlighting promising directions for future work. Theorems 3.9 and 3.11 are the main results of this paper.

**2. The escalator boxcar train.** The EBT method is a numerical scheme for solving physiologically structured population models (PSPMs; see, e.g., [25]). While there are many possible formulations of PSPMs, several of which are described in the excellent book by Metz and Diekmann [25], we consider the numerical solution of the one-dimensional PSPM with a single birth state  $x_b$  defined by (1.1a), (1.1b), and (1.1c). The EBT method determines an approximate measure-valued solution

$\zeta_t^N$  to the PSPM as a linear combination of Dirac measures,

$$\zeta_t^N \equiv \sum_{i=B}^N N_i(t) \delta_{X_i(t)}.$$

Each of the terms in the approximation can be interpreted biologically as a cohort composed of  $N_i$  individuals with average individual state (e.g., size)  $X_i$  at time  $t$ . As individuals give rise to offspring with state  $x_b$  at birth, we need different definitions for *internal cohorts* and the *boundary cohort*.

The internal cohorts are numbered  $i = B + 1, \dots, N$ . These cohorts are chosen at time  $t = 0$  so that  $\zeta_0^N$  converges weakly to the initial data  $u_0(x)dx$  as  $N \rightarrow \infty$ . This is always possible since finite linear combinations of Dirac measures are dense in the weak topology [2, Volume II, p. 214]. Thus, we need not restrict ourselves to initial data prescribed by a function  $u_0(x)$ , but can extend our analysis to general positive Radon measures  $\nu_0$ . Without loss of generality, we will assume that the total mass  $\zeta_0^N([x_b, \infty)) = \nu_0([x_b, \infty))$  for all  $N$ . The boundary cohort is the cohort with the lowest index  $B$ . At time  $t = 0$ ,  $B = 0$  and we assume that  $N_0(0) = 0$  and  $X_0(0) = x_b$ . As time progresses, additional cohorts with negative index will be created through the process of internalization described further below.

The dynamics of the internal cohorts are given by

$$(2.1a) \quad \frac{dN_i}{dt} = -\mu(X_i, \zeta^N) N_i,$$

$$(2.1b) \quad \frac{dX_i}{dt} = g(X_i, \zeta^N),$$

where we have assumed a direct dependence of the vital rates on the solution measure,  $\zeta^N = \zeta_t^N$ , to represent environmental feedback. Similarly, but in contrast to the original formulation of the EBT method by de Roos [7], the dynamics of the boundary cohorts follow:

$$(2.2a) \quad \frac{dN_B}{dt} = -\mu(X_B, \zeta^N) N_B + \sum_{i=B}^N \beta(X_i, \zeta^N) N_i,$$

$$(2.2b) \quad \frac{dX_B}{dt} = g(X_B, \zeta^N),$$

where the sum is taken over all cohorts including the boundary cohort. This sum reflects the offspring produced by the total population. In line with their biological interpretations, we henceforth assume that all vital rates, the mortality rate  $\mu$ , the fecundity rate  $\beta$ , and the growth rate  $g$ , are nonnegative.

With the EBT method defined as above, both the width and the number of individuals in the boundary cohort will increase over time which eventually introduces an unacceptably large approximation error. For this reason, the boundary cohort must be *internalized* sufficiently often. This implies that the number of cohorts will increase following internalization. The new boundary cohort is at the time  $t$  of the internalization given by  $N_B(t) = 0$  and  $X_B(t) = x_b$ , where  $B$  equals the index of the old boundary cohort decremented one step. At the same instant, the previous boundary cohort becomes an internal cohort. To prevent the number of internal cohorts from exceeding computationally acceptable bounds, internal cohorts may be removed when the number of individuals has declined sufficiently. Removal of internal cohorts is important for numerical implementation but will not be considered in this paper.

The EBT method differs from traditional numerical schemes in that it aims to approximate the solution as a measure of point masses. Before we can discuss the convergence of the EBT method, it is necessary to extend the classical concept of a weak solution to measures. This extension builds on earlier work by Gwiazda, Lorenz, and Marciniak-Czochra [18] (see also [4, 19, 27]) and Chapter 8 of the monograph [2]. We will work with the cone of all finite positive Radon measures denoted  $\mathcal{M}_+(\Omega)$ , where  $\Omega$  is a metric space consisting of all admissible individual states. In our presentation, we assume  $\Omega = [x_b, \infty)$  and we think of  $x \in \Omega$  as the size of an individual. An important reason for working with finite Radon measures is that their behavior at infinity is tightly controlled: for each  $\epsilon > 0$ , there exists a compact set  $K_\epsilon$  such that  $\mu(\Omega \setminus K_\epsilon) < \epsilon$ .

Since the EBT method approximates the true solution as a measure of point masses, the natural mode of convergence on  $\mathcal{M}_+(\Omega)$  is *weak convergence*.<sup>1</sup>

DEFINITION 2.1. *A sequence of measures  $\{\mu_k\}$  on  $\Omega$  converges weakly to a measure  $\mu$  if*

$$\int_{\Omega} \phi(x) d\mu_k(x) \rightarrow \int_{\Omega} \phi(x) d\mu(x),$$

as  $k \rightarrow \infty$  for all bounded continuous real functions  $\phi$  on  $\Omega$ .

The weak convergence defined above induces a topology associated with the Kantorovich–Rubinstein metric, also known as the flat metric:

$$\rho(\mu, \nu) = \sup \left\{ \int_{\Omega} \phi(x) d(\mu - \nu) \mid \phi \in C_0^\infty(\mathbb{R}), \|\phi\|_{W^1} \leq 1 \right\},$$

in which  $\|\phi\|_{W^1} = \|\phi\|_L + \|\phi'\|_L$  and  $C_0^\infty(\mathbb{R})$  denotes the space of infinitely differential real-valued functions on  $\mathbb{R}$  with compact support. With this metric,  $\mathcal{M}_+(\Omega)$  is a complete metric space (see [18, Def. 2.5]).

Analogously to weak convergence, we define weak continuity as follows.

DEFINITION 2.2. *A mapping  $\zeta_t : \mathbb{R}_+ \rightarrow \mathcal{M}_+(\Omega)$  is weakly continuous in time if, for all bounded continuous real functions  $\phi$  on  $\Omega$ ,*

$$\int_{\Omega} \phi(x) d\zeta_t$$

is continuous in the classical sense as a function of  $t$ .

With these two topological notions in place, we are in position to define measure-valued solutions to the PSPM (1.1).

DEFINITION 2.3. *A mapping  $\zeta_t : [0, T] \rightarrow \mathcal{M}_+([0, \infty))$  is a weak solution to (1.1) up to time  $T$  if  $\zeta_t$  is weakly continuous in time and*

$$\begin{aligned} & \int_{x_b}^\infty \phi(x, T) d\zeta_T(x) - \int_{x_b}^\infty \phi(x, 0) d\nu_0(x) \\ &= \int_0^T \int_{x_b}^\infty \left( \frac{\partial \phi}{\partial t}(x, t) + g(x, \zeta_t) \frac{\partial \phi}{\partial x}(x, t) - \mu(x, \zeta_t) \phi(x, t) \right) d\zeta_t(x) dt \\ (2.3) \quad &+ \int_0^T \phi(x_b, t) \int_{x_b}^\infty \beta(x, \zeta_t) d\zeta_t(x) dt \end{aligned}$$

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<sup>1</sup>There are two natural notions of convergence on  $\mathcal{M}_+(\Omega)$ —strong convergence and weak convergence. Strong convergence is unsuitable for our purposes as, for example, the sequence of Dirac measures  $\delta_{1/n}$  does not converge to  $\delta_0$  as  $n \rightarrow \infty$  in the strong topology.

for all infinitely differentiable real-valued test functions  $\phi$  on  $\mathbb{R} \times \mathbb{R}$  with compact support, henceforth written  $\phi \in C_0^\infty(\mathbb{R} \times \mathbb{R})$ . Here,  $\nu_0 \in \mathcal{M}_+(\Omega)$  is the initial data at time  $t = 0$ .

*Remark 2.4.* The definition above was inspired by Gwiazda, Lorenz, and Marciniak-Czochra [18]. We differ in that we use smooth test functions, but note that these are dense in the space  $C^1 \cap W^{1,\infty}$  used in [18].

*Remark 2.5.* The dependence on the environmental feedback variable  $E$  in (1.1) is represented here by a direct dependence on the solution measure  $\zeta_t$ .

In order to show the convergence of the EBT method, we will recast the definition of a weak solution. Let  $0 \leq t_1 < t_2 \leq T$  and  $\nu \in \mathcal{M}_+(\Omega)$ . For a given test function  $\phi \in C_0^\infty(\mathbb{R} \times \mathbb{R})$  and a family of measures  $\sigma_t$ , we define the residual

$$(2.4) \quad R_\phi(\sigma_t, \nu, t_1, t_2) = \int_{x_b}^\infty \phi(x, t_2) d\sigma_{t_2}(x) - \int_{x_b}^\infty \phi(x, t_1) d\nu(x) \\ - \int_{t_1}^{t_2} \int_{x_b}^\infty \left( \frac{\partial \phi}{\partial t}(x, t) + g(x, \zeta_t) \frac{\partial \phi}{\partial x}(x, t) - \mu(x, \zeta_t) \phi(x, t) \right) d\sigma_t(x) dt \\ - \int_{t_1}^{t_2} \phi(x_b, t) \left( \int_{x_b}^\infty \beta(x', \zeta_t) d\sigma_t(x') \right) dt,$$

where the measure  $\nu$  is interpreted as the initial data at time  $t = t_1$ . Clearly, if  $R_\phi(\sigma_t, \nu_0, 0, T) = 0$  for all test functions  $\phi$  and the family of measures  $\sigma_t$  is weakly continuous in time, then  $\sigma_t$  is a weak solution to (1.1). We will sometimes write  $R_\phi(\sigma_t)$  meaning  $R_\phi(\sigma_t, \nu_0, 0, T)$ .

**3. Convergence of the escalator boxcar train.** We establish the convergence of the EBT method in five steps: (1) At each fixed time  $t$ , the sequence of approximating EBT measures contains a subsequence which converges weakly to a positive Radon measure  $\zeta_t$ . (2) We find a subsequence that for all  $t$  converges weakly to a mapping  $\zeta_t$  that is weakly continuous in time. (3) The residuals of the approximating EBT measures  $\zeta_t^N$  converges to the residual of  $\zeta_t$  for any test function. (4) The residual of the approximating EBT measures  $\zeta_t^N$  converges to zero, and hence the measure  $\zeta_t$  is a weak solution. All that remains is then to show that the entire sequence of approximating EBT measures converges weakly to  $\zeta_t$ . We do this by (5) assuming the existence of a unique weak solution to the structured population model and showing that a contradiction will otherwise result. The core elements of the proof are the parts required for the fourth step, i.e., Lemmas 3.5 and 3.7 and the estimates needed in section 4 to deal with the original nonlinear transformation at each internalization.

Throughout the proof, we assume that the vital rates  $g$ ,  $\beta$ , and  $\mu$  are nonnegative, continuous, and bounded functions of the state variable  $x$ . We further assume that they are Lipschitz continuous with respect to the measure variable (the feedback from the population-level to the individual vital). Specifically, we assume that

$$\sup_x |\beta(x, \sigma) - \beta(x, \lambda)| \leq C_\beta \rho(\sigma, \lambda), \\ \sup_x |g(x, \sigma) - g(x, \lambda)| \leq C_g \rho(\sigma, \lambda), \\ \sup_x |\mu(x, \sigma) - \mu(x, \lambda)| \leq C_\mu \rho(\sigma, \lambda).$$

Here, the Lipschitz continuity in  $\mathcal{M}_+(\Omega)$  is asserted with respect to the Kantorovich–Rubinstein metric, and the constants are assumed independent of  $x$  as well as the measure variables  $\sigma$  and  $\lambda$ .

LEMMA 3.1 (step 1). *For each  $t \in [0, T]$ , the sequence  $\{\zeta_t^N\}$  of approximating EBT measures contains a weakly convergent subsequence. In fact, any subsequence  $\{\zeta_t^N\}$  of  $\{\zeta_t^N\}$  contains a weakly convergent subsequence.*

*Proof.* By Prohorov’s theorem [2], it is enough to show that the sequence  $\{\zeta_t^N\}$  is uniformly bounded in the variation norm and is uniformly tight. As the measures are positive by construction, this amounts to showing that  $\zeta_t^N([x_b, \infty))$  is uniformly bounded in  $N$ , with  $\lim_{M \rightarrow \infty} \sup_N \zeta_t^N((M, \infty)) = 0$ . A biological interpretation of these requirements, which we will build on in the proof, is that the abundance and typical size of individuals in the population are bounded from above. Letting  $P_N(s) = \zeta_s^N([x_b, \infty))$ , it follows that

$$\begin{aligned} P'_N(s) &= \sum_{i=B}^N N'_i(s) = \sum_{i=B}^N \beta(X_i, \zeta_s^N) N_i(s) - \sum_{i=B}^N \mu(X_i, \zeta_s^N) N_i(s) \\ &\leq \sum_{i=B}^N \beta(X_i, \zeta_s^N) N_i(s) \leq \beta_{\text{sup}} \sum_{i=B}^N N_i(s) = \beta_{\text{sup}} P_N(s), \end{aligned}$$

where  $\beta_{\text{sup}}$  is the supremum of  $\beta$ , i.e., the maximum individual birth rate. The above inequality holds for all  $s \in [0, T]$  except at the finite number of times, where boundary cohorts are internalized. At these points, the function  $P_N$  is continuous. Thus,  $0 \leq P_N(t) \leq P_N(0) \exp(\beta_{\text{sup}} T)$ . Hence  $P_N(t) = \zeta_t^N([x_b, \infty))$  is uniformly bounded on  $[0, T]$ , since  $P_N(0)$  is independent of  $N$ . (Recall that in section 3 we assumed that the initial mass should be independent of  $N$  and equal to that of the population measure given as initial condition.)

To prove  $\lim_{M \rightarrow \infty} \sup_N \zeta_t^N((M, \infty)) = 0$ , we first show that the statement is true for  $t = 0$ . Let  $\varepsilon > 0$  be given. Since the initial data  $\nu_0$  is a positive Radon measure and thus tightly controlled at infinity, we may choose  $M_1$  large enough such that  $\nu_0((M_1, \infty)) < \varepsilon/2$ . Pick any continuous function  $\varphi$  on  $[x_b, \infty)$  satisfying  $0 \leq \varphi(x) \leq 1$  with  $\varphi(x) = 1$  for  $x > M_1 + 1$  and  $\varphi(x) = 0$  for  $x < M_1$ . Then

$$\zeta_0^N([M_1 + 1, \infty)) \leq \int_{M_1}^{\infty} \varphi d\zeta_0^N < \int_{M_1}^{\infty} \varphi d\nu_0 + \varepsilon/2 < \varepsilon,$$

if we choose  $N > N_0$  for some sufficiently large  $N_0$ , since  $\zeta_0^N$  converges weakly to  $\nu_0$  as  $N \rightarrow \infty$ . To account for the measures with  $N \leq N_0$ , we choose  $M_2$  so large that  $\zeta_0^N([M_2, \infty)) < \varepsilon$  for  $N = 1, 2, \dots, N_0$ . Finally, we choose  $M$  as the largest of the two numbers  $M_1 + 1$  and  $M_2$ .

To prove the statement for a general time  $t \in [0, T]$ , we first note that the center of mass and abundance at time  $t$  of any internal cohort  $i > 0$  with  $X_i(t)$  large enough can be estimated with their respective values at time  $t = 0$ . Specifically,  $X_i(t) \leq X_i(0) + tg_{\text{sup}}$ , where  $g_{\text{sup}}$  is the supremum of the growth rate  $g$ , and  $N_i(t) \leq N_i(0)$ . Combining these two estimates, we have that  $\zeta_t^N(M, \infty) \leq \zeta_0^N(M - tg_{\text{sup}}, \infty)$  and the first assertion of the lemma follows. Finally we note that the above argument holds for any subsequence of  $\{\zeta_t^N\}$ . This concludes the proof.  $\square$

LEMMA 3.2 (step 2). *The approximating EBT sequence  $\{\zeta_t^N\}$  contains a subsequence which, for each  $t \in [0, T]$ , converges weakly to a positive finite measure  $\zeta_t$ . The mapping  $\zeta_t : [0, T] \rightarrow \mathcal{M}_+(\Omega)$  is weakly continuous in time.*

*Proof.* Let  $\{q_k\}_{k=1}^{\infty}$  be an enumeration of the rational numbers in  $[0, T]$ . According to Lemma 3.1 there exists a convergent subsequence  $\{\zeta_{q_1}^{N^1}\}$  of  $\{\zeta_t^N\}$ . Repeating this argument, there exists a convergent subsequence  $\{\zeta_{q_2}^{N^2}\}$  of  $\{\zeta_{q_1}^{N^1}\}$ . Proceeding



by induction, we obtain for each  $k$  a sequence  $\{\zeta_{q_k}^{N^k}\}$  which converges weakly to  $\zeta_{q_k}$  and is a subsequence of all preceding sequences. Inspired by Cantor’s diagonalization argument we define the sequence  $\hat{\zeta}_t^k := \zeta_t^{N^k}$ . It follows that for each rational  $t \in [0, T]$ , this sequence converges weakly to a measure  $\zeta_t$ .

We will now show that the subsequence also converges to a positive finite Radon measure for all real  $t \in [0, T]$ . We first show that for each fixed test function  $\phi \in C^\infty(\mathbb{R})$  and each time  $t$ , the sequence of real numbers

$$(3.1) \quad \int_{x_b}^\infty \phi \, d\hat{\zeta}_t^k$$

converges as  $k \rightarrow \infty$ . It then follows from classical results in the theory of distributions, e.g., [22, Theorems 2.1.8 and 2.1.9], that  $\hat{\zeta}_t^k$  converges weakly to a positive measure  $\zeta_t$ . This will turn out to be the desired measure.

To prove convergence of the sequence (3.1), we first note that for fixed  $k$ , the measure  $\hat{\zeta}_t^k$  is weakly continuous in time since each  $N_i(\cdot)$  and  $X_i(\cdot)$  are continuous functions. Let  $t \in [0, T]$  and  $\phi$  be a test function. Given  $\varepsilon > 0$  we get

$$\begin{aligned} & \left| \int_{x_b}^\infty \phi \, d\hat{\zeta}_t^j - \int_{x_b}^\infty \phi \, d\hat{\zeta}_t^k \right| \\ \leq & \left| \int_{x_b}^\infty \phi \, d\hat{\zeta}_t^j - \int_{x_b}^\infty \phi \, d\hat{\zeta}_q^j \right| + \left| \int_{x_b}^\infty \phi \, d\hat{\zeta}_q^j - \int_{x_b}^\infty \phi \, d\hat{\zeta}_q^k \right| + \left| \int_{x_b}^\infty \phi \, d\hat{\zeta}_q^k - \int_{x_b}^\infty \phi \, d\hat{\zeta}_t^k \right| \end{aligned}$$

for any  $j, k$ , and  $q$ . Noting that the birth rate and mortality rate are bounded, we can use the same argument as in the proof of Lemma 3.1 to show that the first and last terms above are bounded by a constant multiple of  $|t - q|$ . In particular, this constant depends on neither  $j$  nor  $k$ . Choosing  $q$  as a rational number sufficiently close to  $t$  these two terms will be smaller than  $\varepsilon/2$ . Finally, since  $q$  is rational, we may choose  $j$  and  $k$  large enough to make the middle term less than  $\varepsilon/2$ . Thus, we have established the Cauchy property for the sequence (3.1), which hence converges for all test functions  $\phi$ . This shows that  $\hat{\zeta}_t^j$  converges weakly to a bounded positive Radon measure  $\hat{\zeta}_t$  for all  $t \in [0, T]$ .

Using the same idea as above, we see that  $\hat{\zeta}_t$  is weakly continuous in time. Specifically,

$$\begin{aligned} & \left| \int_{x_b}^\infty \phi \, d\hat{\zeta}_s - \int_{x_b}^\infty \phi \, d\hat{\zeta}_t \right| \\ \leq & \left| \int_{x_b}^\infty \phi \, d\hat{\zeta}_s - \int_{x_b}^\infty \phi \, d\hat{\zeta}_s^k \right| + \left| \int_{x_b}^\infty \phi \, d\hat{\zeta}_s^k - \int_{x_b}^\infty \phi \, d\hat{\zeta}_t^k \right| + \left| \int_{x_b}^\infty \phi \, d\hat{\zeta}_t^k - \int_{x_b}^\infty \phi \, d\hat{\zeta}_t \right|, \end{aligned}$$

where again the middle term is bounded by a constant multiple of  $|t - s|$  independent of  $k$ . Finally, the first and last terms can be made arbitrarily small as a consequence of the weak convergence of  $\hat{\zeta}_s^k$  to  $\hat{\zeta}_s$ .  $\square$

LEMMA 3.3. *Assume that the sequence  $\zeta_t^k$  converges weakly to a finite Radon measure  $\zeta_t$ . If  $\varphi \in C_0^\infty(\mathbb{R} \times \mathbb{R})$ , then, for every bounded continuous function  $f$  satisfying*

$$\sup_x |f(x, \sigma) - f(x, \lambda)| \leq C_f \rho(\sigma, \lambda)$$

for all  $\sigma, \lambda \in \mathcal{M}_+(\Omega)$ , we get

$$\int_0^T \int_{x_b}^\infty \varphi(x, t) f(x, \zeta_t^k) d\zeta_t^k(x) dt \rightarrow \int_0^T \int_{x_b}^\infty \varphi(x, t) f(x, \zeta_t) d\zeta_t(x) dt,$$

as  $k$  tends to infinity.

*Proof.* We have

$$(3.2) \quad \int_{x_b}^\infty \varphi(x, t) f(x, \zeta_t^k) d\zeta_t^k(x) = \int_{x_b}^\infty \varphi(x, t) f(x, \zeta_t) d\zeta_t^k(x) + \int_{x_b}^\infty \varphi(x, t) (f(x, \zeta_t^k) - f(x, \zeta_t)) d\zeta_t^k(x).$$

By the Portmanteau theorem, the first term on the right-hand side converges to

$$\int_{x_b}^\infty \varphi(x, t) f(x, \zeta_t) d\zeta_t(x).$$

It remains to show that the second term in (3.2) vanishes as  $k \rightarrow \infty$ ,

$$\begin{aligned} & \left| \int_{x_b}^\infty \varphi(x, t) (f(x, \zeta_t^k) - f(x, \zeta_t)) d\zeta_t^k(x) \right| \\ & \leq \sup_x |\varphi(x, t) (f(x, \zeta_t^k) - f(x, \zeta_t))| \zeta_t^k([x_b, \infty)) \\ & \leq \sup_x |\varphi(x, t)| \sup_x |f(x, \zeta_t^k) - f(x, \zeta_t)| \zeta_t^k([x_b, \infty)) \\ & \leq C_\varphi C_f \rho(\zeta_t^k, \zeta_t) \zeta_t^k([x_b, \infty)). \end{aligned}$$

Since  $\zeta_t^k$  converges weakly to  $\zeta_t$ , it follows from Gwiazda, Lorenz, and Marciniak-Czochra [18, Theorem 2.7] that  $\zeta_t^k([x_b, \infty))$  is uniformly bounded and  $\rho(\zeta_t^k, \zeta_t)$  tends to zero as  $k$  tends to infinity. Since the above calculation is done pointwise in  $t$ , the lemma follows from Lebesgue’s dominated convergence theorem.  $\square$

LEMMA 3.4 (step 3). *Assume that the sequence  $\zeta_t^k$  converges weakly to the finite Radon measure  $\zeta_t$ . Then the residual  $R_\phi(\zeta_t^k)$  converges to  $R_\phi(\zeta_t)$  for all test functions  $\phi \in C_0^\infty(\mathbb{R}_+ \times [0, T])$ .*

*Proof.* Consider

$$(3.3) \quad \begin{aligned} R_\phi(\zeta_t^k) &= \int_{x_b}^\infty \phi(x, T) d\zeta_t^k(x) - \int_{x_b}^\infty \phi(x, 0) d\nu_0(x) \\ &\quad - \int_0^T \int_{x_b}^\infty \left( \frac{\partial \phi}{\partial t}(x, t) + g(x, \zeta_t^k) \frac{\partial \phi}{\partial x}(x, t) - \mu(x, \zeta_t^k) \phi(t, x) \right) d\zeta_t^k(x) dt \\ &\quad - \int_0^T \phi(x_b, t) \left( \int_{x_b}^\infty \beta(x', \zeta_t^k) d\zeta_t^k(x') \right) dt = I - II - III - IV. \end{aligned}$$

The first term converges by definition of weak convergence and the second term is unchanged. The third and fourth terms converge by Lemma 3.3.  $\square$

LEMMA 3.5. *Let  $0 \leq t_1 < t_2 \leq T$  and  $v \in \mathcal{M}_+(\Omega)$ . Assuming that no internalization is done in the interval  $(t_1, t_2)$ , then for any test function  $\phi \in C_0^\infty(\mathbb{R} \times \mathbb{R})$  we*

have that

$$R_\phi(\zeta_t^N, \nu, t_1, t_2) = \sum_{i=B}^N N_i(t_1)\phi(X_i(t_1), t_1) - \int_{x_b}^\infty \phi(x, t_1) d\nu(x) - \int_{t_1}^{t_2} (\phi(X_B(t), t) - \phi(x_b, t)) \sum_{i=B}^N \beta(X_i(t), \zeta_t^N) N_i(t) dt,$$

where the sum is taken over all cohorts, including the boundary cohort.

*Proof.* We write the residual (2.4) as

$$\begin{aligned} R_\phi(\zeta_t^N, \nu, t_1, t_2) &= \int_{x_b}^\infty \phi(x, t_2) d\zeta_{t_2}^N(x) - \int_{x_b}^\infty \phi(x, t_1) d\nu(x) \\ &\quad - \int_{t_1}^{t_2} \int_{x_b}^\infty (\phi_2(x, t) + g(x, \zeta_t^N) \phi_1(x, t) - \mu(x, \zeta_t^N)\phi(x, t)) d\zeta_t^N(x) dt \\ &\quad - \int_{t_1}^{t_2} \phi(x_b, t) \left( \int_{x_b}^\infty \beta(x', \zeta_t^N) d\zeta_t^N(x') \right) dt \\ &= I(\zeta_{t_2}^N) - II(\nu) - III(\zeta_t^N) - IV(\zeta_t^N). \end{aligned}$$

Here we have used the shorthand notation  $\phi_1(x, t) = \partial\phi(x, t)/\partial x$  and  $\phi_2(x, t) = \partial\phi(x, t)/\partial t$ .

Recalling that

$$\zeta_t^N = \sum_{i=B}^N N_i(t)\delta_{X_i(t)},$$

we get

$$\begin{aligned} I(\zeta_{t_2}^N) &= \sum_{i=B}^N N_i(t_2)\phi(X_i(t_2), t_2), \\ III(\zeta_t^N) &= \sum_{i=B}^N \int_{t_1}^{t_2} N_i(t) (\phi_2(X_i(t), t) + g(X_i(t), \zeta_t^N) \phi_1(X_i(t), t) \\ &\quad - \mu(x_i(t), \zeta_t^N)\phi(X_i(t), t)) dt \\ &= III_B(\zeta_t^N) + \sum_{i=B+1}^N III_i(\zeta_t^N). \end{aligned}$$

Now, by (2.1), we have

$$\begin{aligned} III_i(\zeta_t^N) &= \int_{t_1}^{t_2} N_i(t) \phi_2(X_i(t), t) + N_i(t) \frac{dX_i(t)}{dt} \phi_1(x_i(t), t) + \frac{dN_i(t)}{dt} \phi(X_i(t), t) dt \\ &= \int_{t_1}^{t_2} \frac{d}{dt} (N_i(t)\phi(X_i(t), t)) dt = N_i(t_2)\phi(X_i(t_2), t_2) - N_i(t_1)\phi(X_i(t_1), t_1). \end{aligned}$$

Thus

$$I(\zeta_{t_2}^N) - \sum_{i=B+1}^N III_i(\zeta_t^N) = N_B(t_2)\phi(X_B(t_2), t_2) + \sum_{i=B+1}^N N_i(t_1)\phi(X_i(t_1), t_1).$$

In the same way, but now also using (2.2), we get

$$\begin{aligned} III_B(\zeta_t^N) &= \int_{t_1}^{t_2} \frac{d}{dt} (N_B(t) \phi(X_B(t), t) - \phi(X_B(t), t) \sum_{i=B}^N \beta(X_i(t), \zeta_t^N) N_i(t)) dt \\ &= N_B(t_2) \phi(X_B(t_2), t_2) - N_B(t_1) \phi(X_B(t_1), t_1) \\ &\quad - \int_{t_1}^{t_2} \phi(X_B(t), t) \sum_{i=B}^N \beta(X_i(t), \zeta_t^N) N_i(t) dt. \end{aligned}$$

Since

$$IV(\zeta_t^N) = \int_{t_1}^{t_2} \phi(x_b, t) \sum_{i=B}^N \beta(X_i(t), \zeta_t^N) N_i(t) dt,$$

we have

$$\begin{aligned} -III_B(\zeta_t^N) - IV(\zeta_t^N) &= -N_B(t_2) \phi(X_B(t_2), t_2) + N_B(t_1) \phi(X_B(t_1), t_1) \\ &\quad + \int_{t_1}^{t_2} (\phi(X_B(t), t) - \phi(x_b, t)) \sum_{i=B}^N \beta(X_i(t), \zeta_t^N) N_i(t) dt. \end{aligned}$$

Summing up the calculations above, we get

$$\begin{aligned} I(\zeta_{t_2}^N) - \sum_{i=B+1}^N III_i(\zeta_t^N) - III_B(\zeta_t^N) - IV(\zeta_t^N) \\ &= N_B(t_2) \phi(X_B(t_2), t_2) + \sum_{i=B+1}^N N_i(t_1) \phi(X_i(t_1), t_1) - N_B(t_2) \phi(X_B(t_2), t_2) \\ &\quad + N_B(t_1) \phi(X_B(t_1), t_1) + \int_{t_1}^{t_2} (\phi(X_B(t), t) - \phi(x_b, t)) \sum_{i=B}^N \beta(X_i(t), \zeta_t^N) N_i(t) dt \\ &= \sum_{i=B}^N N_i(t_1) \phi(X_i(t_1), t_1) + \int_{t_1}^{t_2} (\phi(X_B(t), t) - \phi(x_b, t)) \sum_{i=B}^N \beta(X_i(t), \zeta_t^N) N_i(t) dt. \end{aligned}$$

Finally we get that

$$\begin{aligned} R_\phi(\zeta_t^N, \nu, t_1, t_2) &= \sum_{i=B}^N N_i(t_1) \phi(X_i(t_1), t_1) - \int_{x_b}^\infty \phi(x, t_1) d\nu(x) \\ &\quad + \int_{t_1}^{t_2} (\phi(X_B(t), t) - \phi(x_b, t)) \sum_{i=B}^N \beta(X_i(t), \zeta_t^N) N_i(t) dt. \quad \square \end{aligned}$$

*Remark 3.6.* The residual can be interpreted as the sum of the error arising from the discretization of the initial data and the error arising from the boundary cohort. In the interior of the individual state space, the EBT method gives an exact solution, i.e., there are no errors arising from the transportation of the interior cohorts.

**LEMMA 3.7** (step 4). *With  $\zeta_t^N$  defined by the EBT method with internalizations at times  $t_i = iT/n$ , we have that*

$$R_\phi(\zeta_t^N, \nu_0, 0, T) \rightarrow 0,$$

as  $N$  and  $n$  tend to infinity. Here  $\nu_0$  is the initial data at time  $t = t_0 = 0$ .

*Proof.* We first write

$$R_\phi(\zeta_t^N, \nu_0, 0, T) = R_\phi(\zeta_t^N, \nu_0, 0, t_1) + \sum_{i=1}^{n-1} R_\phi(\zeta_t^N, \zeta_{t_i}^N, t_i, t_{i+1}).$$

By Lemma 3.5 we have

$$\begin{aligned} R_\phi(\zeta_t^N, \nu_0, 0, t_1) &= \sum_{i=B}^N N_i(0)\phi(x_i(0), 0) - \int_{x_b}^\infty \phi(x, 0) d\nu_0(x) \\ &\quad + \int_0^{t_1} (\phi(X_B(t), t) - \phi(x_b, t)) \sum_{i=B}^N \beta(X_i(t), \zeta_t^N) N_i(t) dt \end{aligned}$$

and

$$R_\phi(\zeta_t^N, \zeta_{t_i}^N, t_i, t_{i+1}) = \int_{t_i}^{t_{i+1}} (\phi(X_B(t), t) - \phi(x_b, t)) \sum_{j=B}^N \beta(x_j(t), \zeta_t^N) N_j(t) dt.$$

A straightforward estimate now gives

$$\begin{aligned} |R_\phi(\zeta_t^N, \nu_0, 0, T)| &\leq \left| \sum_{i=B}^N N_i(0)\phi(x_i(0), 0) - \int_{x_b}^\infty \phi(x, 0) d\nu_0(\xi) \right| \\ &\quad + \sum_{i=0}^{n-1} \int_{t_i}^{t_{i+1}} |\phi(X_B(t), t) - \phi(x_b, t)| \sum_{j=B}^N \beta(x_j(t), \zeta_t^N) N_j(t) dt. \end{aligned}$$

The first term tends to zero by assumption as the number of initial cohorts,  $N$ , tends to infinity. Noting that  $x_b = X_B(t_i)$  and using that the growth rate is bounded, we get

$$|\phi(X_B(t), t) - \phi(x_b, t)| \leq C_\phi |X_B(t) - x_b| \leq C_{\phi g} |t - t_i|.$$

Hence,

$$\begin{aligned} \sum_{i=0}^{n-1} \int_{t_i}^{t_{i+1}} |\phi(X_B(t), t) - \phi(x_b, t)| \sum_{j=B}^N \beta(x_j(t), \zeta_t^N) N_j(t) dt \\ \leq \sum_{i=0}^{n-1} C_{\phi g} |t_{i+1} - t_i|^2 C_{\beta\nu_0} \end{aligned}$$

for the constant  $C_{\beta\nu_0} = \beta_{\text{sup}}\nu_0([x_b, \infty)) \exp(\beta_{\text{sup}}T)$ . Thus, the last sum is bounded by  $C(T)/n$  which also tends to zero as the number of internalizations tends to infinity.  $\square$

*Remark 3.8.* Examining the proof above, we see that the residual tends to zero whenever the maximal time between two internalizations of the boundary cohort tends to zero. Hence, we can relax the assumption that the times at which the boundary cohort is internalized are evenly distributed.

Recalling that the initial cohorts are chosen to converge weakly to the initial data, we are now able to prove convergence of the EBT.

**THEOREM 3.9.** *Assume that the assumptions on the birth, growth, and mortality rates in the beginning of section 3 hold. If the structured population model given by (1.1a), (1.1b), and (1.1c) has a unique solution  $\zeta_t$ , then the solutions  $\zeta_t^N$  given by the EBT method converge weakly to  $\zeta_t$  as the number of initial cohorts tends to infinity and the maximal time between two boundary cohort internalizations tends to zero.*

*Proof* (step 5). We assume that the entire sequence  $\zeta_t^N$  does not converge to  $\zeta_t$ . Then, in the weak topology, there exists an open neighborhood  $U$  of  $\zeta_t$ , and a subsequence  $\zeta_t^{N_k}$  of  $\zeta_t^N$  such that  $\zeta_t^{N_k} \notin U$  for all  $N_k$ . From Lemmas 3.1–3.7, we conclude that  $\{\zeta_t^{N_k}\}$  contains a convergent subsequence with a limit point not equal to  $\zeta_t$ , which is a contradiction since it would imply that the solution to the PSPM is not unique.  $\square$

The proof of convergence assumed exact solutions to the ordinary differential equations (ODEs) underlying the EBT method. In practical implementations, these need to be solved numerically which introduces small but finite approximation errors. We now extend the convergence proof to account for errors introduced by the underlying ODE solver.

The following lemma is an immediate consequence of Lemma 3.4.

**LEMMA 3.10.** *Assume that  $\zeta_t^{N,h} = \sum_{i=B}^N N_i^h(t) \delta_{X_i^h(t)}$ . If for each  $t$  we have that  $N_i^h(t) \rightarrow N_i(t)$  and  $X_i^h(t) \rightarrow X_i(t)$  as  $h \searrow 0$ , then  $R_\phi(\zeta_t^{N,h}, \nu_0, 0, T) \rightarrow R_\phi(\zeta_t^N, \nu_0, 0, T)$  as  $h \searrow 0$ .*

Combining the lemma above with Theorem 3.9 we finally have the following theorem.

**THEOREM 3.11.** *Assume that the assumptions on the birth, growth, and mortality rates in the beginning of section 3 hold. If the structured population model given by (1.1a), (1.1b), and (1.1c) has a unique solution  $\zeta_t$ , then the solutions  $\zeta_t^{N,h}$ , given by the numerical integration of the EBT method, converge weakly to  $\zeta_t$  if the number of initial cohorts tends to infinity and the maximal time between two boundary cohort internalizations tends to zero, while  $h$  tends to zero sufficiently fast.*

**4. The original definition of the boundary cohort.** Our study of convergence of the EBT in section 3 assumed different dynamics of the boundary cohorts than was used in the original formulation of the method by de Roos [7]. We based our work on the assumption that the boundary cohort differed from the interior cohorts only in the addition of a term for the inflow of newborns. In this section, we consider the convergence of the EBT method under the original definition of the boundary cohort dynamics.

While we simply assumed a dynamical system for the boundary cohort, de Roos formally derived the underlying equations. Consequently, the original dynamics for the boundary cohort reflect the reduction in center of mass that in reality accompanies an inflow of newborns. Moreover, as the center of mass is not defined as a physical quantity for an empty cohort, the equations were derived through series expansion around the size at birth. Thus, rather than tracking the center of mass  $X_B(t)$  directly, de Roos considered a quantity  $\pi_B$  which roughly represents the cumulative amount by which the individuals in the boundary cohort exceed their birth size. This quantity is mapped onto the center of mass through the nonlinear transformation

$$(4.1) \quad X_B = \begin{cases} \frac{\pi_B}{N_B} + x_b & \text{if } \pi_B > 0, \\ x_b & \text{otherwise.} \end{cases}$$

The specific equations used for defining the boundary cohort were

$$(4.2) \quad \frac{dN_B}{dt} = -\mu(x_b, \zeta^N)N_B - \frac{\partial\mu(x_b, \zeta^N)}{\partial x}\pi_B + \sum_{i=B}^N \beta(X_i, \zeta^N)N_i,$$

$$(4.3) \quad \frac{d\pi_B}{dt} = g(x_b, \zeta^N)N_B + \frac{\partial g(x_b, \zeta^N)}{\partial x}\pi_B - \mu(x_b, \zeta^N)\pi_B,$$

with initial conditions  $N_B = \pi_B = 0$ . We will assume that these are nonnegative, as this is a natural requirement which can easily be enforced by an ODE solver if necessary. The appearance of partial derivatives in the expressions above, arising from series expansion around the size at birth, in conjunction with the nonlinear transformation mapping  $\pi_B$  and  $N_B$  onto  $X_B$ , pose new challenges for proving convergence. As we will show, however, our proof of convergence can be tailored to accompany also the original definition of the boundary cohort.

Note first that the only parts in the proof of convergence in which the equations defining the boundary cohort are used is Lemma 3.5 and implicitly in Theorem 3.11. It, therefore, suffices to give new proofs of these statements. To this end, we require an additional lemma concerning the behavior of the quotient  $\pi_B/N_B$ .

LEMMA 4.1. *With  $N_B$  and  $\pi_B$  defined by (4.2) and (4.3), we get*

$$0 \leq X_B - x_b \leq Ct$$

for  $t \in [t_0, t_0 + h]$  and some positive constants  $C$  and  $h$  which only depend on  $g$ ,  $\partial g/\partial x$ , and  $\partial\mu/\partial x$ .

*Proof.* From the definitions of  $N_B$  and  $\pi_B$  we have

$$\begin{aligned} \frac{d}{dt}X_b &= \frac{d}{dt}\frac{\pi_B}{N_B} = \frac{1}{N_B}\frac{d\pi_B}{dt} - \frac{\pi_B}{N_B^2}\frac{dN_B}{dt} \\ &= g + \frac{\partial g}{\partial x}\frac{\pi_B}{N_B} - \mu\frac{\pi_B}{N_B} + \mu\frac{\pi_B}{N_B} + \frac{\partial\mu}{\partial x}\frac{\pi_B^2}{N_B^2} - \frac{\pi_B}{N_B^2}\sum_{i=B}^N \beta_i N_i \\ &= g + \frac{\partial g}{\partial x}\frac{\pi_B}{N_B} + \frac{\partial\mu}{\partial x}\frac{\pi_B^2}{N_B^2} - \frac{\pi_B}{N_B^2}\sum_{i=B}^N \beta_i N_i \\ &\leq g + \frac{\partial g}{\partial x}\frac{\pi_B}{N_B} + \frac{\partial\mu}{\partial x}\left(\frac{\pi_B}{N_B}\right)^2. \end{aligned}$$

Remembering that  $X_B = \pi_B/N_B + x_b$ , we thus have  $X'_B \leq a + b(X_B - x_b) + c(X_B - x_b)^2$  for some positive constants  $a, b$ , and  $c$ . Hence  $X'_B \leq 2a$  when  $X_B \leq X_B^*$  for some positive  $X_B^*$ . Since  $X_B(0) = x_b$  it follows that  $X_B(t) \leq x_b + 2at$  for  $t \in [0, X_B^*/2a]$ .  $\square$

We now use this to show the following lemma.

LEMMA 4.2. *Assume that a new boundary cohort is created at time  $t = t_1$ . For  $t_2 > t_1$  sufficiently close to  $t_1$ , we have for all  $t \in [t_1, t_2]$  that*

$$(4.4) \quad \left| N_B(t) \left( \frac{dX_B(t)}{dt} - g(X_B(t), \zeta_t^N) \right) \right| \leq C_1(t_2 - t_1)$$

and

$$(4.5) \quad \left| \pi_B(t) \frac{\partial}{\partial x} \mu(X_B(t), \zeta_t^N) \right| \leq C_2(t_2 - t_1).$$

*Proof.* Since  $N_B$  is bounded,  $\pi_B = N_B(X_B - x_b)$ , it follows from the above proof that  $|\pi_B(t)| \leq C(t_2 - t_1)$  for some positive constant  $C$ . Hence, since  $\partial\mu(X_B(t), \zeta_t^N)/\partial x$  is also bounded by the assumptions in [7], the statement (4.5) follows trivially. To show the first part of the assertion, we note that

$$N_B(t) \left( \frac{dX_B(t)}{dt} - g(X_B(t), \zeta_t^N) \right) = \frac{\partial g}{\partial x} \pi_B + \frac{\partial \mu}{\partial x} \pi_B \frac{\pi_B}{N_B} - \frac{\pi_B}{N_B} \sum_{i=B}^N \beta_i N_i.$$

Since  $\pi_B$  and  $\pi_B/N_B = X_B - x_b$  both increase at most linearly from zero, the assertion (4.4) follows.  $\square$

The two lemmas above will be used to bound the residual between two internalizations.

LEMMA 4.3. *Let  $0 \leq t_1 < t_2 \leq T$  and  $\nu \in \mathcal{M}_+(\Omega)$ . For a given test function  $\phi \in C_0^\infty(\mathbb{R} \times \mathbb{R})$  and a family of measures  $\sigma_t$ . Assuming that no internalization is done in the interval  $(t_1, t_2)$ , then*

$$\begin{aligned} R_\phi(\zeta_t^N, \nu, t_1, t_2) &= \sum_{i=B}^N N_i(t_1) \phi(X_i(t_1), t_1) - \int_{x_b}^\infty \phi(x, t_1) d\nu(x) \\ &+ \int_{t_1}^{t_2} (\phi(X_B(t), t) - \phi(x_b, t)) \sum_{i=B}^N \beta(X_i(t), \zeta_t^N) N_i(t) dt \\ &+ \int_{t_1}^{t_2} N_B(t) \left( \frac{dX_B(t)}{dt} - g(X_B(t), \zeta_t^N) \right) \phi_1(X_B(t), t) \\ &+ (\mu_1(X_B(t), \zeta_t^N) \pi_B(t)) \phi(X_B(t), t) dt, \end{aligned}$$

where the sums are taken over all cohorts, including the boundary cohort.

*Proof.* Examining the proof of Lemma 3.5 we see that the boundary cohort only appears in the term  $III_B$ ,

$$\begin{aligned} III_B(\zeta_t^N) &= \int_{t_1}^{t_2} N_B(t) (\phi_1(X_B(t), t) + g(X_B(t), \zeta_t^N) \phi_1(X_B(t), t) \\ &- \mu(X_B(t), \zeta_t^N) \phi(X_B(t), t)) dt. \end{aligned}$$

This term is shown to be equivalent with

$$\int_{t_1}^{t_2} \frac{d}{dt} (N_B(t) \phi(X_B(t), t) - \phi(X_B(t), t) \sum_{i=B}^N \beta(X_i(t), \zeta_t^N) N_i(t)) dt.$$

Using the original definition for the boundary cohort dynamics, (4.2) and (4.3), we derive the required correction term

$$\begin{aligned} &\int_{t_1}^{t_2} \frac{d}{dt} (N_B(t) \phi(x_B(t), t) - \phi(X_B(t), t) \sum_{i=B}^N \beta(X_i(t), \zeta_t^N) N_i(t) dt - III_B(\zeta_t^N) \\ &= \int_{t_1}^{t_2} N_B(t) \left( \frac{dX_B(t)}{dt} - g(x_B(t), \zeta_t^N) \right) \phi_1(X_B(t), t) \\ &+ \mu_1(X_B(t), \zeta_t^N) \pi_B(t) \phi(X_B(t), t) dt. \quad \square \end{aligned}$$



By Lemma 4.2, we see that the correction term above is bounded by  $C(t_2 - t_1)^2$ . Analogous to Lemma 3.7, we then have the following lemma.

LEMMA 4.4. *With  $\zeta_t^N$  defined by the EBT method with internalizations at times  $t_i = iT/n$ , we have that*

$$R_\phi(\zeta_t^N, \nu_0, 0, T) \rightarrow 0,$$

as  $N$  and  $n$  tend to infinity. Here  $\nu_0$  is the initial data at time  $t = t_0 = 0$ .

The original definition of the boundary cohorts might prove more challenging from a numerical perspective. However, if we can determine numerically solutions  $\zeta_t^{N,h}$  to the equations of the EBT method such that the center of mass,  $X_B^h$ , now determined by the nonlinear transformation (4.1) converges to its true value,  $X_B$ , as the step length  $h \searrow 0$ , the residual still tends to zero according to Lemma 3.10. Hence, the numerical convergence follows as before.

**5. Discussion.** Enhanced biological realism and predictive ability of theoretical investigations are gaining importance as anthropogenic impacts are fundamentally altering the native environment of many organisms. Physiologically structured population models (PSPMs) are increasingly used to model and analyze biological systems. As these models account for the physiological development of individuals, they are better able to predict system dynamics. In contrast to simple unstructured population models such as the classical Lotka–Volterra equations, PSPMs often defy analytical investigations due to the nonlocal dependencies. There is thus a mounting need for numerical methods that can effectively uncover the underlying dynamics. The Escalator Boxcar Train (EBT) has been specifically designed for PSPMs and has three major advantages: it prevents numerical diffusion, it is relatively easy to implement, and the underlying equations allow for a natural biological interpretation. The method was developed more than two decades ago and has been used to study PSPMs ever since, but the fact that convergence has never been formally proved might well have hampered its wider acceptance beyond the domains of theoretical biology.

In this paper we have given the first rigorous proof of convergence for the EBT method. Our proof is given in a modern setting of measure-valued solutions (see e.g., [18]). This contrasts with previous efforts by de Roos and Metz [9] that were carried out in a classical setting and thus required additional smoothness assumptions. While their efforts fell short of proving the full convergence of the EBT method, the authors succeeded in showing that the method consistently approximates the true solution, i.e., that the local approximation error as measured through an arbitrary (but smooth) functional of the solution is bounded and vanishes in the limit of infinitely fine discretization of the individual state space. Our study also complements the existing convergence analyses of particle methods for first-order hyperbolic equations, reviewed by [6] and thoroughly analyzed in [27], by demonstrating that particle methods can be brought to bear on equations which renew themselves at the boundary. Having been placed on a solid theoretical foundation, particle methods with the added ingredient of frequent internalizations now stand an excellent chance of being adopted as the method of choice for a rapidly expanding array of exciting biological applications.

There are many possible extensions of the work presented here. A straightforward extension is to write down the corresponding proof for a higher-dimensional state space but with a single birth state. We believe that with more tedious calculations, one could prove the convergence also for the case of stochastic birth state. A further extension is to consider different versions of the boundary cohort dynamics and internalization. We initially proved convergence when the boundary cohort dif-

fers only by the addition of a fecundity term. While this works mathematically, it is natural to account for the fact that newborn individuals reduce the average size of individuals in the boundary cohort. The original formulation of the EBT method does account for this through a different definition of the boundary cohort, and as a second step we analyzed and proved convergence for that case. We believe that our proof can be extended to show convergence also for other formulations of the boundary cohort, as long as the flux of individuals is preserved in the limit of frequent internalizations. A more challenging extension is to consider stochasticity in individual development which on the population-level roughly amounts to diffusion. Here, important insights and ideas could be derived from the rich literature on particle methods, in which many different partial differential equations (PDEs) with specific nonlocal dependencies have been analyzed (see, e.g., [1, 5, 6, 16, 23, 28]). It would also be very interesting to consider the problem of multiple birth states, with the typical example being cell division. A final important extension would be to consider vital rates that depend on the entire history of the population state up to the current time, rather than merely the current population state, as this would encompass cases with dynamic environmental feedback variables.

For practical numerical applications, it would be very useful to have estimates on the rate of convergence under different smoothness assumptions. Such estimates might also inform the choice of boundary cohort dynamics. Also here, insights and ideas could be derived from the rich literature of particle methods, although it is not obvious how the techniques used there to assess convergence rates should be adapted and tailored to our methodology of proof. The standard method for deriving estimates of convergence rates for particle approximations of transport equations considers two solutions to the transport equation with different initial conditions and follows the characteristic curves back to the initial data in order to estimate how much they differ. Choosing one of these two solutions as the particle approximation now yields an error estimate. This method does not work in our setting, however, as we can neither follow the characteristic curves back to the initial data, nor substitute the particle approximation as one of the two solutions. Partial results in this direction have, however, already been obtained in [4] using an operator-splitting algorithm from semigroup theory. The authors prove continuous dependence with respect to parameters and initial data for a broad range of equations that include our nonconservative problem (1.1). In the absence of births, i.e., if  $\beta \equiv 0$ , their result yields an estimate of the error of the approximate solution at a later time. It is quite possible that the techniques in [4] could be used to establish an independent convergence proof for the EBT method, but it would require additional machinery such as regular internalizations to overcome the complications that arise at the boundary as individuals start to grow into the domain. If this effort could be successfully carried out, it would almost certainly yield estimates of the convergence rate. Moreover, it would be a major step forward for the understanding of particle methods in biology and other fields with nonconservative equations.

Given the long tradition of PDEs in the physical sciences, it is not surprising that PSPMs were initially studied using this formalism. Efforts in the last few decades have revealed, however, that the PDE formalism is not always well suited for considering questions of existence, uniqueness, and stability. For this reason, the cumulative formulation of structured population models [15, 13] was developed. It had the drawback, however, that a principle of linearized stability and the Hopf bifurcation theorem proved hard to establish [20]. Currently, it appears that renewal equations are well suited for studying PSPMs [11, 12, 14, 20]. The work presented here has been de-

veloped from the PDE setting. We believe, however, that renewal equations are a promising framework for developing and analyzing numerical methods for PSPMs. A first step would be to recast the EBT method in this setting, after which the extensions outlined above could be considered. With interest in PSPMs now mounting, a historical opportunity exists for bridging biological theory and computational mathematics through the development of modern numerical methods for the 21st century.

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