

DIFFUSION OF BIOLOGICAL ORGANISMS; FICKIAN AND FOKKER-PLANCK TYPE DIFFUSIONS

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ABSTRACT. In this paper we derive diffusion equations in a heterogeneous environment. We consider a system of discrete kinetic equations that consists of two phenotypes of different turning frequencies. The two phenotypes change their states according to state transition frequencies which depend on environment. We show that the density of the total population of the two phenotypes converges to the solution of a Fokker-Planck type diffusion equation if turning frequencies are of higher order than the state transition frequencies. If it is the other way around, i.e., if the state is changed many times between each turning, the density converges to the solution of a Fickian diffusion equation.

1. INTRODUCTION

The random dispersal of minute particles suspended in fluid is often mathematically modeled by a diffusion equation. The same diffusion equation is also taken to model the random migration of biological organisms and successfully provides fundamental insights into the role of migration in the context of spatial ecology (see [4, 23, 28]). The purpose of this paper is to develop a diffusion model based on the behavior of individual biological organisms instead of simply adopting a diffusion model for Brownian particles. In this way we hope to obtain a better diffusion theory that explains dispersal phenomena of biological organisms correctly.

The main difference between biological organisms and Brownian particles is in the way to adapt to spatial and temporal variation of environments. If the environment is homogeneous, the difference is neutralized and the two would show the same dispersal phenomenon. Therefore, we need to consider heterogeneous environments to understand a biologically meaningful dispersal. In fact, the reason for biological organisms to migrate is to find a better place for living and hence a biological diffusion theory in a homogeneous environment is an oversimplification. Indeed, many researchers emphasized the importance of formulating a realistic dispersal theory for biological species that takes into account interactions between individuals and responses to environmental variations (see Skellam [29, 30] and Okubo & Levin [23, Chapter 5]).

There have been many efforts and discussions to find a correct diffusion equation for physical particles in heterogeneous environments. For example, if temperature is spatially heterogeneous, Brownian particles often aggregate and form a nonconstant steady state. This phenomenon is called by many names such as the thermal diffusion, thermophoresis, or Soret effect. For such a case the diffusivity is spatially nonconstant, i.e., $D = D(\mathbf{x})$. Three diffusion models are often considered:

$$\begin{aligned} (1) \quad & u_t = \nabla \cdot (D(\mathbf{x})\nabla u), \\ (2) \quad & u_t = \nabla \cdot (\sqrt{D(\mathbf{x})}(\nabla \sqrt{D(\mathbf{x})}u)), \\ (3) \quad & u_t = \Delta(D(\mathbf{x})u), \end{aligned}$$

which are all identical if the diffusivity is constant. Equation (1) is called Fick's law and any constant state is a steady state. Equations (2) and (3) were derived by Wereide [34] and Chapman [6], respectively, and steady states are nonconstant if the diffusivity is not constant. The three equations are also satisfied by the probability density function of

a stochastic process when the variation of jumping distance, denoted by $|\Delta x|^2$, depends on the terminal, middle, or starting point of each jump, respectively, in the order. In other words, (2) and (3) are obtained by the Stratonovich and Ito integrals of a stochastic process, respectively. Note that in the three cases of stochastic processes, the jumping time, denoted by Δt , is spatially homogeneous. If both of Δx and Δt are spatially heterogeneous, another diffusion equation,

$$(4) \quad u_t = \nabla \cdot \alpha(\mathbf{x}) \nabla(v(\mathbf{x})u),$$

has been considered in [7], where $v(\mathbf{x}) = \frac{\Delta x}{\Delta t}$ and $\alpha(\mathbf{x}) = D(\mathbf{x})/v(\mathbf{x})$. If Δt is constant, (2) and (4) are identical to each other. The Fickian type diffusion (1) and the Fokker-Planck type one (3) are often compared as mathematical dispersal models for physical particles and biological species in heterogeneous environment (see [3, 33]).

The diffusion model for biological species requires extra ingredients to include the adaptation ability to environmental heterogeneity. The adaptation ability is often based on a simple mechanism. For example, many species often increase their motility and move to another place if starvation started. If the departing probability, denoted by γ , depends on the information where they live, the corresponding diffusion equation is given by (6). Even if they do not know the direction for a better place and hence their migration is completely random and unbiased, such a behavior may increase their chance for survival (see [7]). These strategies have been developed through the natural selection process and only successful ones are selected (see [19, 20]).

In this paper, we develop a biological diffusion model as a diffusion limit of an unbiased discrete kinetic equations of a microscopic (or mesoscopic) scale level. Understanding the connection between macroscopic scale collective phenomena we observe and the microscopic scale individual behavior biological traits dictate has been one of main goals of mathematical modeling. In particular, the connection between macroscopic model and microscopic or mesoscopic scale kinetic model attracted much attention recently. For example, a link between Keller-Segel type macroscopic scale chemotaxis equations and individual bacterium level kinetic models has been intensively examined (see [1, 5, 12, 13, 14, 24]). In these models individuals are assumed to sense the chemical *gradient* and changes their turning frequencies depending on the gradient direction. It is such a bias that produces a chemotactic drift. In this context, the approach of this paper is quite different since individuals do not sense the chemical gradient and hence the random walk system is unbiased.

The key idea comes from Funaki *et al.* [10] which considers a model with two sub-population groups of different diffusion rates. We apply the idea into the context of discrete kinetic equations. In n space dimensions, the system consists of $4n$ equations (7)-(8). For simplicity, we consider one space dimension first, where the system is written as

$$(5) \quad \begin{cases} \partial_t u_+ + \frac{1}{\epsilon} \partial_x u_+ = \frac{\omega_u}{\epsilon^2} (u_- - u_+) + \frac{\eta}{\epsilon^2} (g v_+ - f u_+), \\ \partial_t u_- - \frac{1}{\epsilon} \partial_x u_- = \frac{\omega_u}{\epsilon^2} (u_+ - u_-) + \frac{\eta}{\epsilon^2} (g v_- - f u_-), \\ \partial_t v_+ + \frac{1}{\epsilon} \partial_x v_+ = \frac{\omega_v}{\epsilon^2} (v_- - v_+) + \frac{\eta}{\epsilon^2} (f u_+ - g v_+), \\ \partial_t v_- - \frac{1}{\epsilon} \partial_x v_- = \frac{\omega_v}{\epsilon^2} (v_+ - v_-) + \frac{\eta}{\epsilon^2} (f u_- - g v_-). \end{cases}$$

Here, u_+ and v_+ are population densities that moves to right and u_- and v_- are the ones to left. The partial sums, $u := u_+ + u_-$ and $v := v_+ + v_-$, are population densities of two population groups with different turning frequencies ω_u and ω_v , respectively, and $\rho := u + v$ is the total population. We regard the turning frequencies as their dispersal

strategies and assume that they are constants such that

$$0 < \omega_v < \omega_u,$$

i.e., u is the state that the species turns more frequently.¹ The assumption that a species changes its turning frequency depending on the environmental variation is widely accepted. For example, Keller and Segel [17] derived their chemotaxis model under the assumption that a species increases its turning frequency when the signaling chemical is abundant. Starvation driven dispersal is another example, where the two phenotypes represent stuffed and hungry individuals. It is observed that a ladybug reduces its turning rate when it is hungry (see [16]).

The coefficients, $f = f_{u \rightarrow v}$ and $g = g_{v \rightarrow u}$, are state transition frequencies between the two population groups. Note that it is the ability of transition between two groups with different dispersal strategies that gives extra adaptation ability to biological organisms when the environment is spatially and temporally variant. The value of this paper is in comparing the biological diffusion obtained by the effect of this state transition and the particle diffusion represented by (1)–(3). The other coefficients, ε and η , are scaling parameters and we consider solution sequences $u_{\varepsilon, \eta}$, $v_{\varepsilon, \eta}$ and $\rho_{\varepsilon, \eta}$. We took ε as the parameter for diffusion scaling and we will take the limit as $\varepsilon \rightarrow 0$. The other parameter η is to compare the size of the state transition and the turning frequencies. The meaningful case is when $\omega_u, \omega_v \gg \eta$, i.e., an individual changes its moving direction many times before a state transition occurs. The opposite case, $\omega_u, \omega_v \ll \eta$, implies that the state of an individual changes many times between two consecutive directional turn. In the case, dividing the population into two groups of different turning frequencies becomes meaningless and the whole population behaves as a single group.

The advection parts have velocity of $\pm \frac{1}{\varepsilon}$ for both phenotypes. However, if one phenotype changes its moving direction more frequently, its mean speed drops due to its time consumption during tumbling and acceleration processes. Note that the effect of reduced speed is not included in this paper and the both phenotypes are assumed to have the same speed.²

We will find diffusion limits of $4n$ equations (7)–(8) in n -space dimensions. The diffusion equation corresponding to the meaningful case of $\omega_u, \omega_v \gg \eta$ is obtained by taking limit $(\varepsilon, \eta) \rightarrow (0, 0)$ with $\eta/\varepsilon^2 \rightarrow \infty$. We show that the limit satisfies a Fokker-Planck type diffusion equation,

$$\rho_t = \Delta(\gamma(\rho, \mathbf{x})\rho), \quad \rho := \lim_{(\varepsilon, \eta) \rightarrow (0, 0)} \rho_{\varepsilon, \eta},$$

where $\gamma(\rho, \mathbf{x})$ is given by (11). This Fokker-Planck type diffusion equation can be written into two parts,

$$\rho_t = \nabla \cdot \left(\left(\gamma + \rho \frac{\partial \gamma}{\partial \rho} \right) \nabla \rho + \rho \nabla_{\mathbf{x}} \gamma \right),$$

where $(\gamma + \rho \frac{\partial \gamma}{\partial \rho}) \nabla \rho$ is a Fickian type diffusion term and $\rho \nabla_{\mathbf{x}} \gamma(\rho, \mathbf{x})$ is an advection term.

We also take the limit $(\varepsilon, \eta) \rightarrow (0, \infty)$ for the case of $\omega_u, \omega_v \ll \eta$ and show that the limit satisfies a Fickian type diffusion equation,

$$\rho_t = \nabla \cdot (\tilde{\gamma}(\rho, \mathbf{x}) \nabla \rho), \quad \rho := \lim_{(\varepsilon, \eta) \rightarrow (0, \infty)} \rho_{\varepsilon, \eta},$$

¹One may extend the theory to nonconstant and nonlinear turning frequencies such as $\omega_u = \omega_u(u, \mathbf{x})$ and $\omega_v = \omega_v(v, \mathbf{x})$ following the method in [8] and [21]. However, we will focus on the nonlinearity and spatial heterogeneity in the state transition frequencies f and g since these are the ones that decide the type of diffusion.

²The effect of reduced speed could be critical. For example, the density of Brownian particles is reversely proportional to the speed. Therefore, the reduction of mean speed can induce a population aggregation.

where $\tilde{\gamma}(\rho, \mathbf{x})$ is given by (11). In this case there is no advection phenomenon. If $(\epsilon, \eta) \rightarrow (0, \ell^2)$ for some constant $\ell > 0$, the limit satisfies a diffusion equation (14) which is a combination of the previous two.

The approach developed in this paper can be applied to various situations if the whole population is split into two or more groups with different dispersal strategies and the transition from one group to another is allowed. In Section 7, we apply this idea to derive the starvation driven diffusion, or SDD for brevity, from this kinetic model by splitting the population with two groups of hungry and stuffed ones. The SDD is a dispersal model of a biological species given by

$$(6) \quad \rho_t = \Delta(\gamma(s)\rho),$$

where $\gamma(s)$ is the departing probability which is an increasing function of a starvation measure s (see [7, 18, 19, 20]). In this situation, u and v represent population density who are stuffed or starved, respectively. The assumption $0 < \omega_v \leq \omega_u$ implies that the hungry population, v , change the moving direction less frequently. The state transition phenomenon in this case is the one that a hungry individual becomes stuffed one or vice versa. If a hungry one consumes enough food or a stuffed one does not consume food for a while, then the state transition occurs.

We may take the following ratios as starvation measures:

$$s := s_u + s_v = \frac{\rho}{2nm}, \quad \text{where} \quad s_u := \frac{u}{2nm}, \quad s_v := \frac{v}{2nm},$$

where $m = m(\mathbf{x})$ is a food (or resource) distribution and n is the space dimension. The ratio $\frac{m}{\rho}$ is the amount of resource per population which measures how favorable the environment is. Hence, its reciprocal $\frac{\rho}{m}$ measures starvation of the species. We multiply $\frac{1}{2n}$ and take $s = \frac{\rho}{2nm}$ for a notational convenience in a later use. Finally, we take transition frequencies as functions of starvation measures given by

$$f(\tau, \mathbf{x}) = \hat{f}\left(\frac{\tau}{m(\mathbf{x})}\right) \quad \text{and} \quad g(\tau, \mathbf{x}) = \hat{g}\left(\frac{\tau}{m(\mathbf{x})}\right),$$

where the spatial heterogeneity comes from the nonconstant food distribution $m(\mathbf{x})$. We assume that the ratio of hungry population v increases if the starvation measure increases, i.e.,

$$\frac{v}{u} = \frac{\hat{f}(s_u)}{\hat{g}(s_v)} \uparrow \quad \text{as} \quad s \uparrow \infty, \quad \text{where} \quad \hat{f}(s_u) = f\left(\frac{u}{2n}, \mathbf{x}\right), \quad \hat{g}(s_v) = g\left(\frac{v}{2n}, \mathbf{x}\right).$$

Then, as the starvation measure increases, the average dispersal rate of the species increases and hence the species may migrate more.

The analytical component of this paper is in proving diffusion limits of the discrete kinetic model. Whenever we look for a hydrodynamic or relaxation limit for a small parameter $\epsilon \rightarrow 0$, a uniform estimate of the solution sequence is necessary. For kinetic models, obtaining a uniform estimate of the flux ($J_{i,j}^{u,\epsilon} := \frac{u_i - u_j}{\epsilon}$ in our case) is the key. Since the state transition frequencies, f and g , are spatially heterogeneous and nonlinear, we choose an energy functional reflecting these situations and show such an estimate in Section 4. Then, a strong convergence of solutions in the limit is shown in Section 5 using the div-curl lemma. In Section 6, we identify flux terms, $J_{i,j}$'s and H_i 's, and find the limiting diffusion equation that ρ satisfies in the three cases. The existence theory of a solution to the kinetic equations follows from the semigroup theory outlined in [11, 25] and is introduced in Section 3. We have obtained diffusion limits when f and g are given. The last question is about the existence of state transition frequencies, f and g , that produces a given Fokker-Planck type diffusion equation $\rho_t = \Delta(\gamma(\rho, \mathbf{x})\rho)$. We show that there is a one to one correspondence between (f, g) and γ in an admissible and normalized class of functions in Section 7.

2. NOTATION AND MAIN RESULTS

In this section we introduce the discrete kinetic model of the paper in multi-space dimensions and our main results. Since many quantities and indexes appear in the paper, it is important to be consistent in notation. We take a rectangular domain with periodic boundary conditions. The space dimension is n and we consider $2n$ number of directions. The population density is divided into $2n$ fractional ones. For example, u_{k+} is the population density of a phenotype u that moves to the positive direction of the k -th coordinate. We will reserve indexes i and j to denote these $2n$ directions, i.e., $i, j = 1\pm, \dots, n\pm$. The space dimension will be denoted by k , the sequence index by h , and a subsequence one by l .

Let $Q = [-1, 1]^n \subset \mathbb{R}^n$, $Q_T = Q \times (0, T)$, and $Q_\infty = Q \times (0, \infty)$. Consider a system of $4n$ equations for u_i^ε and v_i^ε for $i = 1\pm, \dots, n\pm$;

$$(7) \quad \frac{\partial}{\partial t} u_i + \frac{1}{\varepsilon} \mathbf{e}_i \cdot \nabla u_i = \frac{\omega_u}{2n\varepsilon^2} \sum_{j=1\pm}^{n\pm} (u_j - u_i) + \frac{1}{\delta^2} (g(v_i, \mathbf{x})v_i - f(u_i, \mathbf{x})u_i),$$

$$(8) \quad \frac{\partial}{\partial t} v_i + \frac{1}{\varepsilon} \mathbf{e}_i \cdot \nabla v_i = \frac{\omega_v}{2n\varepsilon^2} \sum_{j=1\pm}^{n\pm} (v_j - v_i) + \frac{1}{\delta^2} (f(u_i, \mathbf{x})u_i - g(v_i, \mathbf{x})v_i),$$

where $(\mathbf{x}, t) \in Q_\infty$. The parameter η in (5) corresponds to ε^2/δ^2 . Let $u_{k\pm}$ and $v_{k\pm}$ be fractional population densities of the two population groups that move to directions $\mathbf{e}_{k\pm} := \pm \mathbf{e}_k$, respectively. We will denote the solution using a vector notation, $\mathbf{u}_\pm := (u_{1\pm}, \dots, u_{n\pm})$ and $\mathbf{v}_\pm := (v_{1\pm}, \dots, v_{n\pm})$ if needed. We consider the problem with initial values and periodic boundary conditions, for $i = 1\pm, \dots, n\pm$,

$$(9) \quad u_i(\mathbf{x}, 0) = u_{i,0}(\mathbf{x}), \quad v_i(\mathbf{x}, 0) = v_{i,0}(\mathbf{x}),$$

$$(10) \quad u_i(\mathbf{x}_1, t) = u_i(\mathbf{x}_2, t), \quad v_i(\mathbf{x}_1, t) = v_i(\mathbf{x}_2, t) \quad \text{if } (\mathbf{x}_2 - \mathbf{x}_1) \in [2\mathbb{Z}]^n.$$

The initial values are also denoted by $(\mathbf{u}_\pm, \mathbf{v}_\pm)(0)$ or $(\mathbf{u}_{\pm,0}, \mathbf{v}_{\pm,0})$ using a vector notation. Denote

$$J_{i,j}^{u,\varepsilon} = \frac{u_i - u_j}{\varepsilon}, \quad J_k^{u,\varepsilon} = J_{k+,k-}^{u,\varepsilon}, \quad \mathbf{J}^{u,\varepsilon} = (J_1^{u,\varepsilon}, J_2^{u,\varepsilon}, \dots, J_n^{u,\varepsilon}),$$

which are called fluxes of u . The fluxes of v are similarly denoted. The fluxes of the whole species ρ are defined as the sum of the two, i.e.,

$$J_{i,j}^{\rho,\varepsilon} = J_{i,j}^{u,\varepsilon} + J_{i,j}^{v,\varepsilon}, \quad J_k^{\rho,\varepsilon} = J_k^{u,\varepsilon} + J_k^{v,\varepsilon}, \quad \mathbf{J}^{\rho,\varepsilon} = \mathbf{J}^{u,\varepsilon} + \mathbf{J}^{v,\varepsilon}.$$

These are fluxes related to the turning dynamics. Similar quantities corresponding to state transition are denoted by

$$H_i^\delta = \frac{f(u_i, \mathbf{x})u_i - g(v_i, \mathbf{x})v_i}{\delta}.$$

Note that, in (7) and (8), f and g depend only on the fractional populations $u_{i\pm}$ and $v_{i\pm}$ for an analysis convenience. However, through the randomness, such a dependency turns into the one on the total population after taking the limit $\varepsilon \rightarrow 0$.

Equations (7) and (8) describe the dispersal dynamics of population when a species has two migration states. We define the solution of the above periodic boundary initial value problem in a weak sense. The uniqueness and the existence of the weak solution could be shown on a broader class of initial value, $L^2(Q_T)$. If the initial value is smooth enough to have derivatives, then this weak solution is actually a strong solution of the problem.

Definition 2.1. Let f and $g: \mathbb{R}^+ \times Q \rightarrow \mathbb{R}^+$ be periodic in $\mathbf{x} \in Q$, $\tau f(\tau, \mathbf{x})$ and $\tau g(\tau, \mathbf{x})$ be $C^1(\mathbb{R}^+ \times Q)$,

$$\tilde{f}(\tau, \mathbf{x}) := \partial_\tau(\tau f(\tau, \mathbf{x})), \quad \text{and} \quad \tilde{g}(\tau, \mathbf{x}) := \partial_\tau(\tau g(\tau, \mathbf{x})).$$

We call f and g are admissible state transition frequencies if \tilde{f} and \tilde{g} are bounded, bounded away from zero, and $\nabla_{\mathbf{x}}f$ and $\nabla_{\mathbf{x}}g$ are uniformly bounded, i.e., if there exists a constant $M > 1$ such that

- (1) $M^{-1} \leq \tilde{f}(\tau, \mathbf{x}), \tilde{g}(\tau, \mathbf{x}) \leq M$, and
- (2) $\|\nabla_{\mathbf{x}}\tau f(\tau, \mathbf{x})\|, \|\nabla_{\mathbf{x}}\tau g(\tau, \mathbf{x})\| \leq M|\tau|$,

where $\|\cdot\|$ denotes the uniform norm in this paper.

Remark 2.2. The functions $\tau \rightarrow \tau f(\tau, \mathbf{x})$ and $\tau \rightarrow \tau g(\tau, \mathbf{x})$ only need to be defined for $\tau \geq 0$. For a notational convenience, we extend them for $\tau \in \mathbb{R}$ into odd functions

$$-\tau f(-\tau, \mathbf{x}) = -\tau f(\tau, \mathbf{x}), \quad -\tau g(-\tau, \mathbf{x}) = -\tau g(\tau, \mathbf{x}),$$

which are used in Proposition 5.4 and Lemma 7.1. Note that $\tau f(\tau, \mathbf{x})$ and $\tau g(\tau, \mathbf{x})$ are now $C^1(\mathbb{R} \times Q)$, and (1)-(2) in Definition 2.1 hold in $\mathbb{R} \times Q$.

Since \tilde{f} and \tilde{g} are bounded away from zero, $\tau \rightarrow \tau f(\tau, \mathbf{x})$ and $\tau \rightarrow \tau g(\tau, \mathbf{x})$ are strictly increasing function in τ . Therefore, for any given $(\rho, \mathbf{x}) \in \mathbb{R}^+ \times Q$ and admissible transition frequencies f and g , there exists a unique positive pair (u, v) such that

$$u + v = \rho, \quad \frac{u}{2n} f\left(\frac{u}{2n}, \mathbf{x}\right) = \frac{v}{2n} g\left(\frac{v}{2n}, \mathbf{x}\right).$$

Using the pair we define

$$(11) \quad \begin{aligned} \gamma(\rho, \mathbf{x}) &:= \frac{1}{n} \left[\frac{1}{\omega_u} \frac{g(v/2n, \mathbf{x})}{f(u/2n, \mathbf{x}) + g(v/2n, \mathbf{x})} + \frac{1}{\omega_v} \frac{f(u/2n, \mathbf{x})}{f(u/2n, \mathbf{x}) + g(v/2n, \mathbf{x})} \right], \\ \tilde{\gamma}(\rho, \mathbf{x}) &:= \frac{1}{n} \left[\omega_u \frac{\tilde{g}(v/2n, \mathbf{x})}{\tilde{f}(u/2n, \mathbf{x}) + \tilde{g}(v/2n, \mathbf{x})} + \omega_v \frac{\tilde{f}(u/2n, \mathbf{x})}{\tilde{f}(u/2n, \mathbf{x}) + \tilde{g}(v/2n, \mathbf{x})} \right]^{-1}. \end{aligned}$$

Notice that $\rho\gamma(\rho, \mathbf{x})$ and $\tilde{\gamma}(\rho, \mathbf{x})$ are in $C^k(\mathbb{R}^+ \times Q)$ and $C^{k-1}(\mathbb{R}^+ \times Q)$, respectively, if $\tau f(\tau, \mathbf{x})$ and $\tau g(\tau, \mathbf{x})$ are in $C^k(\mathbb{R}^+ \times Q)$ for $k \geq 1$ (see Proposition 7.2).

Finally, we introduce the main theorem of the paper.

Theorem 2.3 (Diffusion Limit). *Let f and g be admissible transition frequencies and $\tau f(\tau, \mathbf{x})$ and $\tau g(\tau, \mathbf{x})$ be $C^2(\mathbb{R}^+ \times Q)$. Let $(\varepsilon_h, \delta_h) \rightarrow (0, 0)$ and $(u_{i,0}^h, v_{i,0}^h) \rightarrow (u_{i,0}, v_{i,0})$ in $[L^4(Q)]^{4n}$ as $h \rightarrow \infty$. Then, the weak solutions (u_i^h, v_i^h) of the boundary value problem (7)–(10) with these parameters and initial values converge to the same limit $(\frac{u}{2n}, \frac{v}{2n})$, the mean of their sums, i.e., for all $T > 0$,*

$$u_i^h \rightarrow \frac{u}{2n} \text{ and } v_i^h \rightarrow \frac{v}{2n} \text{ in } L^2(Q_T) \text{ as } h \rightarrow \infty.$$

Therefore,

$$\sum_{i=1\pm}^{n\pm} u_i^h \rightarrow u \text{ and } \sum_{i=1\pm}^{n\pm} v_i^h \rightarrow v \text{ in } L^2(Q_T) \text{ as } h \rightarrow \infty.$$

Furthermore,

$$(12) \quad \frac{u}{2n} f\left(\frac{u}{2n}, \mathbf{x}\right) = \frac{v}{2n} g\left(\frac{v}{2n}, \mathbf{x}\right),$$

and the limit of total population $\rho := u + v$ satisfies the following diffusion equations:

(i) If $\lim_{h \rightarrow \infty} \varepsilon_h / \delta_h = 0$, ρ is the unique weak solution of

$$(13) \quad \rho_t = \Delta(\gamma(\rho, \mathbf{x})\rho).$$

(ii) If $\lim_{h \rightarrow \infty} \varepsilon_h / \delta_h = \ell \in (0, \infty)$, ρ is the unique weak solution of

$$(14) \quad \rho_t = \nabla \cdot \left[\left(1 + \frac{\tilde{f}}{\omega_u} \ell^2 + \frac{\tilde{g}}{\omega_v} \ell^2 \right)^{-1} \nabla(\gamma(\rho, \mathbf{x})\rho) + \left(\frac{n\omega_u\omega_v}{(\tilde{f} + \tilde{g})\ell^2} + \frac{1}{\tilde{\gamma}(\rho, \mathbf{x})} \right)^{-1} \nabla\rho \right],$$

where $\tilde{f}(\mathbf{x}, t) = \tilde{f}(u(\mathbf{x}, t)/2n, \mathbf{x})$ and $\tilde{g}(\mathbf{x}, t) = \tilde{g}(v(\mathbf{x}, t)/2n, \mathbf{x})$.

(iii) If $\lim_{h \rightarrow \infty} \varepsilon_h / \delta_h = \infty$, ρ is the unique weak solution of

$$(15) \quad \rho_t = \nabla \cdot (\tilde{\gamma}(\rho, \mathbf{x}) \nabla \rho).$$

The Fokker-Planck type diffusion equation (13) has nonlinearity and spatial heterogeneity together. In particular, the spatial heterogeneity produces an advection phenomenon as written by

$$\rho_t = \nabla \cdot \left((\gamma + \rho \partial_\rho \gamma) \nabla \rho + \rho \nabla \gamma \right).$$

A constant state is not a steady state solution due to the spatial dependency in $\gamma(\rho, \mathbf{x})$, but not to the nonlinearity. Having a spatial heterogeneity is crucial since it gives a chance to adapt to environment.

Notice that the transport and tumbling terms in the kinetic equations system are unbiased and there is no directional information. However, the state transition phenomenon decides the proportion of the two population groups, u and v , in a spatially heterogeneous way according to the relation (12) and the advection phenomenon comes out of it. On the other hand, the Fickian type diffusion equation (15) does not contain any advection phenomenon even if the proportion is still given by the same relation. Remember that the state of an individual changes a lot of times between two consecutive turns and the heterogeneity in the proportion of u and v does not have any meaning in this case. Find that we may recover (13) and (15) from (14) by taking a limit $\ell \rightarrow 0$ and $\ell \rightarrow \infty$, respectively. The solution convergence as $\ell \rightarrow 0$ or $\ell \rightarrow \infty$ is not shown.

Remark 2.4 (Regularity). *We assume $\tau f(\tau, \mathbf{x})$ and $\tau g(\tau, \mathbf{x})$ are $C^2(\mathbb{R}, Q)$ to ensure the C^2 regularity of $\gamma(\rho, \mathbf{x})\rho$ (c.f. Proposition 7.2) and hence the uniqueness of the weak solution of (13). Until the last paragraph of Section 6, the proof is still valid with only C^1 assumption and we obtain convergence along a subsequence of weak solutions.*

Remark 2.5 (Uniform bounds). *It is clear from (11) that γ and $\tilde{\gamma}$ are bounded by*

$$(16) \quad \frac{1}{n\omega_u} < \gamma(\rho, \mathbf{x}), \quad \tilde{\gamma}(\rho) < \frac{1}{n\omega_v}.$$

Therefore, Eq. (34) is satisfied for some $\varepsilon > 0$ and we have obtained the existence of admissible transition frequencies f and g that produce the given motility function γ . Note that equality holds for (16) if $f = g = 0$ or $\tilde{f} = \tilde{g} = 0$ which are excluded in Definition 2.1.

3. EXISTENCE AND UNIQUENESS

Existence of a solution to the discrete kinetic equations (7)–(10) follows a classical semigroup theory and we briefly introduce it (see [11, 25] for details). For an easier application of the theory, we rewrite the equations in a classical form as follows. Let $X = (u_{1+}, u_{1-}, \dots, v_{1+}, \dots, v_{n-}) \in [L^p(Q)]^{4n}$ for $p \geq 1$. Then, equations (7)–(8) are written as

$$\frac{\partial}{\partial t} X = AX + BX + G(X),$$

where

$$AX = \begin{pmatrix} -\partial_1 u_{1+} \\ \vdots \\ \partial_n u_{n-} \\ -\partial_1 v_{1+} \\ \vdots \\ \partial_n v_{n-} \end{pmatrix}, \quad BX = \begin{pmatrix} \omega_u \sum_{j=1\pm}^{n\pm} u_j - u_{1+} \\ \vdots \\ \omega_u \sum_{j=1\pm}^{n\pm} u_j - u_{n-} \\ \omega_v \sum_{j=1\pm}^{n\pm} v_j - v_{1+} \\ \vdots \\ \omega_v \sum_{j=1\pm}^{n\pm} v_j - v_{n-} \end{pmatrix},$$

and

$$G(X) = \begin{pmatrix} g(v_{1+}, \cdot)v_{1+} - f(u_{1+}, \cdot)u_{1+} \\ \vdots \\ g(v_{n-}, \cdot)v_{n-} - f(u_{n-}, \cdot)u_{n-} \\ f(u_{1+}, \cdot)u_{1+} - g(v_{1+}, \cdot)v_{1+} \\ \vdots \\ f(u_{n-}, \cdot)u_{n-} - g(v_{n-}, \cdot)v_{n-} \end{pmatrix}.$$

Here, the partial derivative $\frac{\partial}{\partial x_k}u$ is denoted by $\partial_k u$. The domain of the linear functional $A : D(A) \rightarrow [L^p(Q)]^{4n}$ is

$$D(A) = \left\{ (u_{1+}, \dots, v_{n-}) \in [L^p(Q)]^{4n} \left| \begin{array}{l} \partial_k u_{k+}, \partial_k u_{k-}, \partial_k v_{k+}, \partial_k v_{k-} \in L^p(Q), \\ u_{k\pm}, v_{k\pm} \text{ are periodic in the } k\text{th direction} \end{array} \right. \right\},$$

which is dense in $[L^p(Q)]^{4n}$. The operators A and B are linear and G is nonlinear. One may check that A is dissipative and there exists $\lambda_0 > 0$ such that the range of $\lambda_0 I - A$ is in $[L^p(Q)]^{4n}$ (see [11, Section 3]). Therefore, the linear operator A generates a strongly continuous semigroup of contraction, $T(t)$ for $t \geq 0$, in $[L^p(Q)]^{4n}$ (see [25, Theorem 4.3 in Section 1]).

On the other hand, B is bounded and G is uniformly Lipschitz in $[L^p(Q)]^{4n}$ if f and g are admissible transition frequencies. Therefore, we may apply Theorem 1.2 in [25, Section 6] and obtain a unique mild solution $w \in C([0, T], [L^p(Q)]^{4n})$ for all $T > 0$ if $w_0 \in [L^p(Q)]^{4n}$. The mapping $w_0 \mapsto w$ is Lipschitz continuous. Here, a mild solution w is the one that satisfies

$$w(t) = T(t)w_0 + \int_0^t T(t-s)(Bw(s) + G(w(s)))ds.$$

Finally, $Bw + G(w) \in C([0, T], [L^p(Q)]^{4n})$ and hence we apply the main theorem of [2] to conclude that w is the unique weak solution.

4. FLUX ESTIMATES USING ENERGY FUNCTIONAL

In this section we derive a priori estimates in L^2 -norm for $J_{i,j}$ and H_i in terms of the initial value which is similar to energy estimate for parabolic equations. These estimates are uniform with respect to ε and δ and are main steps to show the convergence of the three diffusion limits in Theorem 2.3. To manage the spatial heterogeneity in f and g , we start with an appropriate energy functional.

Definition 4.1. *Let $\psi : \mathbb{R} \rightarrow \mathbb{R}$ be a convex function. For a given transition frequency $f : \mathbb{R}^+ \times Q \rightarrow \mathbb{R}^+$ and a population density $w : Q \times \mathbb{R}^+ \rightarrow \mathbb{R}^+$, we define the energy functional by*

$$\mathcal{E}_f(w)(t) := \int_Q \Psi_f(w(\mathbf{x}, t), \mathbf{x}) d\mathbf{x} \quad \text{with} \quad \Psi_f(w, \mathbf{x}) := \int_0^w \psi(\tau f(\tau, \mathbf{x})) d\tau.$$

The total energy of the solutions of the 4n equations, (7)–(10), is defined by

$$\mathcal{E}(\mathbf{u}_\pm, \mathbf{v}_\pm) := \sum_{i=1\pm}^{n\pm} [\mathcal{E}_f(u_i) + \mathcal{E}_g(v_i)].$$

We take $\psi(s) = |s|^\kappa$ with $\kappa \geq 1$ in this paper.

Proposition 4.2. *Let (u_i, v_i) , $i = 1\pm, \dots, n\pm$, be smooth solutions of (7)–(10). Then, for any fixed $T > 0$,*

- (1) *There exists $C_T(\kappa, n, Q) > 0$ such that for all $t \in [0, T]$,*
- $$(17) \quad \mathcal{E}(\mathbf{u}_\pm, \mathbf{v}_\pm)(t) \leq C_T [1 + \mathcal{E}(\mathbf{u}_\pm, \mathbf{v}_\pm)(0)].$$

(2) There exists an upper bound $L_T(\|u_{i,0}\|_{L^2(Q)}, \|v_{i,0}\|_{L^2(Q)}, n, Q) > 0$ such that

$$(18) \quad \sum_{i,j=1\pm}^{n\pm} \left[\|J_{i,j}^{u,\varepsilon}\|_{L^2(Q_T)}^2 + \|J_{i,j}^{v,\varepsilon}\|_{L^2(Q_T)}^2 \right] + \sum_{i=1\pm}^{n\pm} \|H_i^\delta\|_{L^2(Q_T)}^2 \leq L_T.$$

Proof. Multiply $\psi(u_i f(u_i, \mathbf{x}))$ and $\psi(v_i g(v_i, \mathbf{x}))$ to (7) and (8), respectively, integrate the sum of the $4n$ equations over the domain Q , and obtain

$$(19) \quad \begin{aligned} \frac{\partial}{\partial t} \mathcal{E}(\mathbf{u}_\pm, \mathbf{v}_\pm) &= -\frac{1}{\varepsilon} \sum_{i=1\pm}^{n\pm} \int \mathbf{e}_i \cdot \nabla_{\mathbf{x}} [\Psi_f(u_i(\mathbf{x}, t), \mathbf{x}) + \Psi_g(v_i(\mathbf{x}, t), \mathbf{x})] d\mathbf{x} \\ &\quad + \frac{1}{\varepsilon} \sum_{i=1\pm}^{n\pm} \int \mathbf{e}_i \cdot \frac{\partial}{\partial \mathbf{x}} [\Psi_f(u_i, \mathbf{x}) + \Psi_g(v_i, \mathbf{x})] d\mathbf{x} \\ &\quad - \frac{\omega_u}{4n\varepsilon^2} \sum_{i,j=1\pm}^{n\pm} \int (\psi(u_i f(u_i, \mathbf{x})) - \psi(u_j f(u_j, \mathbf{x}))) (u_i - u_j) d\mathbf{x} \\ &\quad - \frac{\omega_v}{4n\varepsilon^2} \sum_{i,j=1\pm}^{n\pm} \int (\psi(v_i g(v_i, \mathbf{x})) - \psi(v_j g(v_j, \mathbf{x}))) (v_i - v_j) d\mathbf{x} \\ &\quad - \frac{1}{\delta^2} \sum_{i=1\pm}^{n\pm} \int (\psi(u_i f(u_i, \mathbf{x})) - \psi(v_i g(v_i, \mathbf{x}))) (u_i f(u_i, \mathbf{x}) - v_i g(v_i, \mathbf{x})) d\mathbf{x}. \end{aligned}$$

The fifth term on the right side is negative since ψ is an increasing function. Furthermore, since $\tau f(\tau, \mathbf{x})$ and $\tau g(\tau, \mathbf{x})$ are increasing functions with respect to τ , the third and fourth terms are also negative. The first term vanishes due to the divergence theorem and the boundary condition. Therefore, the only term left is the second one and we estimate it to obtain (18). We start with the first part of the second term.

$$\begin{aligned} \sum_{i=1\pm}^{n\pm} \frac{1}{\varepsilon} \int \mathbf{e}_i \cdot \frac{\partial}{\partial \mathbf{x}} \Psi_f(u_i, \mathbf{x}) d\mathbf{x} &= \frac{1}{\varepsilon} \sum_{i=1}^n \int \mathbf{e}_i \cdot \frac{\partial}{\partial \mathbf{x}} [\Psi_f(u_{i+}, \mathbf{x}) - \Psi_f(u_{i-}, \mathbf{x})] d\mathbf{x} \\ &= \frac{1}{\varepsilon} \sum_{i=1}^n \int \mathbf{e}_i \cdot \frac{\partial}{\partial \mathbf{x}} \left(\int_{u_{i-}}^{u_{i+}} \psi(\tau f(\tau, \mathbf{x})) d\tau \right) d\mathbf{x} \\ &= \frac{1}{\varepsilon} \sum_{i=1}^n \iint_{u_{i-}}^{u_{i+}} \mathbf{e}_i \cdot \frac{\partial}{\partial \mathbf{x}} (\psi(\tau f(\tau, \mathbf{x}))) d\tau d\mathbf{x} \\ &\leq \frac{1}{\varepsilon} \sum_{i=1}^n \int \left| \int_{u_{i-}}^{u_{i+}} \psi'(\tau f(\tau, \mathbf{x})) \cdot \left\| \frac{\partial}{\partial \mathbf{x}} (\tau f(\tau, \mathbf{x})) \right\| d\tau \right| d\mathbf{x} \\ &\leq \frac{1}{\varepsilon} \sum_{i=1}^n \int \left| \int_{u_{i-}}^{u_{i+}} \kappa (M\tau)^{\kappa-1} M\tau d\tau \right| d\mathbf{x} \\ &\leq \sum_{i=1}^n \int \kappa M^\kappa (u_{i+} + u_{i-})^\kappa \left| \frac{u_{i+} - u_{i-}}{\varepsilon} \right| d\mathbf{x} \\ &\leq \sum_{i=1}^n \int 4\lambda (M(u_{i+} + u_{i-}))^{\kappa+1} d\mathbf{x} + \int \frac{\kappa^2}{\lambda} (M(u_{i+} + u_{i-}))^{\kappa-1} \left| \frac{u_{i+} - u_{i-}}{\varepsilon} \right|^2 d\mathbf{x}, \end{aligned}$$

where $\lambda > 0$. We use $\tau f(\tau, \mathbf{x}) \in C^1$ in the third line. Next, the second term in the last line can be controlled by the third term of (19) as the following. Consider

$$\begin{aligned}
& -\frac{\omega_u}{4n\varepsilon^2} \sum_{i,j=1\pm}^{n\pm} \int \left(\psi(u_i f(u_i, \mathbf{x})) - \psi(u_j f(u_j, \mathbf{x})) \right) (u_i - u_j) d\mathbf{x} \\
& = -\sum_{i,j=1\pm}^{n\pm} \int \frac{\omega_u}{4n\varepsilon^2} \frac{\psi(u_i f(u_i, \mathbf{x})) - \psi(u_j f(u_j, \mathbf{x}))}{u_i f(u_i, \mathbf{x}) - u_j f(u_j, \mathbf{x})} \times \\
& \quad (u_i f(u_i, \mathbf{x}) - u_j f(u_j, \mathbf{x})) (u_i - u_j) d\mathbf{x} \\
& \leq -\sum_{i,j=1\pm}^{n\pm} \int \frac{\omega_u}{4n} \psi' \left(\frac{u_i f(u_i, \mathbf{x}) + u_j f(u_j, \mathbf{x})}{2} \right) \frac{1}{M} \left| \frac{u_i - u_j}{\varepsilon} \right|^2 d\mathbf{x} \\
& \leq -\sum_{i,j=1\pm}^{n\pm} \int \frac{\kappa\omega_u}{4nM(2M)^{\kappa-1}} (u_i + u_j)^{\kappa-1} \left| \frac{u_i - u_j}{\varepsilon} \right|^2 d\mathbf{x}.
\end{aligned}$$

By taking $\lambda(\omega_u, \omega_v, \kappa, n)$ large, we obtain the desired estimate. Same relations hold for the second part of the second term and we finally obtain

$$\begin{aligned}
(20) \quad \frac{\partial}{\partial t} \mathcal{E}(\mathbf{u}_{\pm}, \mathbf{v}_{\pm}) & \leq \sum_{i=1}^n \int 4\lambda(M(u_{i+} + u_{i-}))^{\kappa+1} + 4\lambda(M(v_{i+} + v_{i-}))^{\kappa+1} d\mathbf{x} \\
& - \sum_{i,j=1\pm}^{n\pm} \int \frac{\kappa\omega_u}{8nM} \left(\frac{u_i + u_j}{2M} \right)^{\kappa-1} \left| \frac{u_i - u_j}{\varepsilon} \right|^2 d\mathbf{x} \\
& - \sum_{i,j=1\pm}^{n\pm} \int \frac{\kappa\omega_v}{8nM} \left(\frac{v_i + v_j}{2M} \right)^{\kappa-1} \left| \frac{v_i - v_j}{\varepsilon} \right|^2 d\mathbf{x} \\
& - \sum_{i=1\pm}^{n\pm} \int \left(\psi(u_i f(u_i, \mathbf{x})) - \psi(v_i g(v_i, \mathbf{x})) \right) \frac{u_i f(u_i, \mathbf{x}) - v_i g(v_i, \mathbf{x})}{\delta^2} d\mathbf{x}.
\end{aligned}$$

Since $\Psi_f(u_i(\mathbf{x}), \mathbf{x}) = \int_0^{u_i(\mathbf{x})} (\tau f(\tau, \mathbf{x}))^{\kappa} d\tau \geq \int_0^{u_i(\mathbf{x})} \left(\frac{\tau}{M}\right)^{\kappa} d\tau = \frac{1}{M^{\kappa}} \frac{u_i^{\kappa+1}}{\kappa+1}$, we can bound the first term by a constant times of $\sum_{i=1\pm}^{n\pm} [\mathcal{E}_f(u_i) + \mathcal{E}_g(v_i)]$. Therefore, we can apply Gronwall's inequality to obtain the first conclusion (1). The second one (2) would follow directly from the first one when $\kappa = 1$ and time integration of (20). \square

Corollary 4.3. *If $u_{i,0}, v_{i,0} \in L^p(Q)$ for $i = 1\pm, \dots, n\pm$, then $u_i, v_i \in L^p(Q)$ for $i = 1\pm, \dots, n\pm$, and*

$$\|(\mathbf{u}_{\pm}, \mathbf{v}_{\pm})(t)\|_{[L^p(Q)]^{4n}} \leq C'_T (1 + \|(\mathbf{u}_{\pm}, \mathbf{v}_{\pm})(0)\|_{[L^p(Q)]^{4n}}) \quad \text{for } t \leq T.$$

Proof. Choose $\psi(s) = |s|^{\kappa}$ and notice that $\frac{1}{M^{\kappa}} \frac{u_i^{\kappa+1}}{\kappa+1} \leq \Psi_f(u_i(\mathbf{x}), \mathbf{x}) \leq M^{\kappa} \frac{u_i^{\kappa+1}}{\kappa+1}$. Then, the above follows from the energy estimate. \square

Proposition 4.4. *Let (u_i, v_i) be the unique weak solutions of the equation (7)–(10) with initial values in $L^2(Q)$. Then, (17) in Proposition 4.2 still holds.*

Proof. As mentioned in the existence theorem,

$$(21) \quad (\mathbf{u}_{\pm,0}, \mathbf{v}_{\pm,0}) \mapsto (\mathbf{u}_{\pm}, \mathbf{v}_{\pm})$$

is a Lipschitz continuous mapping from $[L^2(Q)]^{4n}$ into $C([0, T], [L^2(Q)]^{4n})$. We can pick a sequence of smooth, periodic initial values $(u_{i,0}^{\ell}, v_{i,0}^{\ell})$ such that

$$u_{i,0}^{\ell} \rightarrow u_{i,0}, \quad v_{i,0}^{\ell} \rightarrow v_{i,0} \quad \text{in } L^2(Q) \quad \text{as } \ell \rightarrow \infty.$$

Then, the solutions (u_i^l, v_i^l) with the smooth initial values are smooth and

$$u_i^l \rightarrow u_i, \quad v_i^l \rightarrow v_i \quad \text{in } C([0, T], L^2(Q)) \quad \text{as } l \rightarrow \infty$$

due to the Lipschitz continuity of the mapping (21). The flux terms in (17) also converge to the flux terms related to (u_i, v_i) in $C([0, T], [L^2(Q)]^{4n})$. Therefore, we can pass to the limit and have the same estimate for weak solutions. \square

5. CONVERGENCE

In this section we show the convergence in Theorem 2.3. We take a superscript to denote quantities related to scaling parameters $(\varepsilon_h, \delta_h)$ as in u_i^h and $J_{i,j}^{u,h}$. First, we obtain a weakly convergent solution subsequence as a consequence of Proposition 4.2 and Corollary 4.3.

Corollary 5.1. *Let u_i^h and v_i^h satisfy (7)–(10) with scaling parameters $(\varepsilon_h, \delta_h) \rightarrow 0$ as $h \rightarrow \infty$ and uniformly bounded initial values $u_{i,0}^h$ and $v_{i,0}^h$ in $L^2(Q)$. Then, there is a weakly convergent subsequences $u_i^{h_l}$ and $v_i^{h_l}$ (or simply u_i^l and v_i^l) such that, for any $T > 0$,*

$$\begin{aligned} u_i^l &\rightharpoonup u_i, & v_i^l &\rightharpoonup v_i & \text{in } L^2(Q_T) \\ J_{i,j}^{u,l} &\rightharpoonup J_{i,j}^u, & J_{i,j}^{v,l} &\rightharpoonup J_{i,j}^v & \text{in } L^2(Q_T) \end{aligned}$$

and

$$H_i^l = \frac{u_i^l f(u_i^l, \mathbf{x}) - v_i^l g(v_i^l, \mathbf{x})}{\delta_l} \rightharpoonup H_i \text{ in } L^2(Q_T).$$

Proof. The uniform estimate of $\sum_{i=1\pm}^{n\pm} [\mathcal{E}_{1,f}(u_{i,0}^h) + \mathcal{E}_{1,g}(v_{i,0}^h)]$ gives a uniform $L^2(Q_T)$ bound of all sequences above and we can find a weakly convergent subsequence using classical diagonal arguments. \square

Lemma 5.2 (Div-Curl Lemma [22]). *For an open set $A \subset \mathbb{R}^{n+1}$, let w^l and η^l be two sequences such that*

$$\begin{aligned} w^l &\rightharpoonup w \text{ weakly in } [L^2(A)]^{n+1}, \\ \eta^l &\rightharpoonup \eta \text{ weakly in } [L^2(A)]^{n+1}, \end{aligned}$$

$$\begin{aligned} \operatorname{div}(w^l) &\text{ is bounded in } L^2(A) \text{ or compact in } H^{-1}(A), \text{ and} \\ \operatorname{curl}(\eta^l) &\text{ is bounded in } [L^2(A)]^{(n+1)^2} \text{ or compact in } [H^{-1}(A)]^{(n+1)^2}. \end{aligned}$$

Then

$$\langle w^l, \eta^l \rangle \longrightarrow \langle w, \eta \rangle \text{ in distribution sense,}$$

where $\langle \cdot, \cdot \rangle$ denotes the inner product in \mathbb{R}^{n+1} .

Choose $A = Q_T \subset \mathbb{R}^{n+1}$, $w^l = (\mathbf{J}^l, \rho^l)$, and $\eta^l = (0, \rho^l)$ in $[L_{x,t}^2(Q_T)]^{n+1}$. Then,

$$(22) \quad \operatorname{div}_{x,t} w^l = \operatorname{div}_{x,t} (\mathbf{J}^l, \rho^l) = \operatorname{div}_x \mathbf{J}^l + \partial_t \rho^l = 0,$$

which is obtained by adding (7) and (8) over all indices. The curl operator, defined by $(\operatorname{curl} F)_{ij} = \frac{\partial F_i}{\partial x_j} - \frac{\partial F_j}{\partial x_i}$, becomes

$$\operatorname{curl} \eta^l = \begin{pmatrix} 0 & \cdots & 0 & -\partial_{x_1} \rho^l \\ \vdots & \ddots & \vdots & \vdots \\ 0 & \cdots & 0 & -\partial_{x_n} \rho^l \\ \partial_{x_1} \rho^l & \cdots & \partial_{x_n} \rho^l & 0 \end{pmatrix}.$$

We now show that each entry of the matrix is compact in $H^{-1}(A)$. Consider the equations in (7) and (8). If we subtract the equation for $i = k-$ from the one for $i = k+$ and multiply ε_l to it, we obtain

$$(23) \quad \begin{cases} \varepsilon_l^2 \partial_t J_k^{u,l} + \partial_k(u_{k+}^l + u_{k-}^l) = -\omega_u J_k^{u,l} + \frac{\varepsilon_l}{\delta_l} (H_{k-}^l - H_{k+}^l), \\ \varepsilon_l^2 \partial_t J_k^{v,l} + \partial_k(v_{k+}^l + v_{k-}^l) = -\omega_v J_k^{v,l} + \frac{\varepsilon_l}{\delta_l} (H_{k+}^l - H_{k-}^l). \end{cases}$$

Here, the equation has been simplified using the relation of

$$\frac{1}{2n\varepsilon_l} \sum_{j=1\pm}^{n\pm} [\omega_u(u_j^l - u_{k+}^l) - \omega_u(u_j^l - u_{k-}^l)] = \frac{1}{2n} \sum_{j=1\pm}^{n\pm} [-\omega_u J_k^{u,l}] = -\omega_u J_k^{u,l}.$$

Add the two equations in (23) and get H_i^l 's cancelled. Moreover, we have the convergence,

$$\varepsilon_l^2 \partial_t \mathbf{J}^{u,l} \rightarrow 0 \quad \text{and} \quad \varepsilon_l^2 \partial_t \mathbf{J}^{v,l} \rightarrow 0 \quad \text{in} \quad H^{-1}(A),$$

and the compactness of

$$\omega_u \frac{(u_j^l - u_i^l)}{\varepsilon_l} \quad \text{and} \quad \omega_v \frac{(v_j^l - v_i^l)}{\varepsilon_l} \quad \text{in} \quad H^{-1}(A),$$

which are from the uniform $L^2(A)$ boundedness of $J_{i,j}^{u,l}$ and $J_{i,j}^{v,l}$. Thus, we conclude that

$$\partial_k(u_{k+}^l + u_{k-}^l + v_{k+}^l + v_{k-}^l)$$

are compact in $H^{-1}(A)$. Denote $\rho_k^l := u_{k+}^l + u_{k-}^l + v_{k+}^l + v_{k-}^l$. Using the total population ρ^l , we may write

$$\partial_k \rho_k^l = \frac{1}{n} \partial_k \rho^l + \sum_{m=1}^n \frac{1}{n} \partial_k (\rho_k^l - \rho_m^l).$$

Since

$$\rho_k^l - \rho_m^l = \varepsilon_l (J_{k+,m+}^{u,l} + J_{k-,m-}^{u,l} + J_{k+,m+}^{v,l} + J_{k-,m-}^{v,l}) \rightarrow 0 \text{ in } L^2(A),$$

$\partial_k \rho^l$ is compact in $H^{-1}(A)$. Now we are able to apply div-curl lemma which gives the following proposition.

Proposition 5.3. *If initial values $u_{i,0}$ and $v_{i,0}$ are in $L^4(Q)$, then there is a subsequence such that, for all $T > 0$ and $k = 1, \dots, n$,*

$$\rho_k^l \rightarrow \frac{1}{n} \rho \quad \text{in} \quad L^2(Q_T).$$

Proof. Since $[L^4(Q)]^{4n} \subset [L^2(Q)]^{4n}$, Corollary 4.3 implies that

$$\rho_k^l \rightharpoonup \rho_k \quad \text{weakly in} \quad L^2(Q_T).$$

Since $(\rho_k^l - \rho_m^l) \rightarrow 0$ in $L^2(Q_T)$, we have $\rho_k = \frac{1}{n} \rho$ for some $\rho \in L^2(Q_T)$. Next, the div-curl lemma implies that

$$(\rho_k^l)^2 \rightarrow \left(\frac{1}{n} \rho\right)^2 \quad \text{in distribution sense.}$$

The uniform boundedness of $(\rho_k^l)^2$ and $(\frac{1}{n} \rho)^2$ in L^2 , which comes from Corollary 4.3 with $p = 4$, improves above convergence into

$$\left(\rho_i^l\right)^2 \rightharpoonup \left(\frac{1}{n} \rho\right)^2 \quad \text{in } L^2(Q_T).$$

The strong L^2 convergence comes from [26, Lemma 7] which states:

$$\text{If } |A| < \infty, \rho^l \rightharpoonup \rho \text{ and } (\rho^l)^2 \rightharpoonup \rho^2 \text{ in } L^2(A), \text{ then } \rho^l \rightarrow \rho \text{ in } L^2(A).$$

□

Next, we will show that u^l and v^l converge strongly in L^2 as well.

Proposition 5.4. *Under the conditions of Proposition 5.3, $u_i^l \rightarrow u/2n$, $v_i^l \rightarrow v/2n$ strongly in $L^2(Q_T)$ for all $T > 0$ along a subsequence. The fractional populations, u and v , and the total population, $\rho = u + v$, satisfy*

$$u = \left(\frac{g\left(\frac{v}{2n}, \mathbf{x}\right)}{g\left(\frac{v}{2n}, \mathbf{x}\right) + f\left(\frac{u}{2n}, \mathbf{x}\right)} \right) \rho.$$

Proof. We have already obtained

$$u_i^l - u_j^l \rightarrow 0, \quad v_i^l - v_j^l \rightarrow 0, \quad \rho^l = u^l + v^l \rightarrow \rho, \quad \text{and} \quad \delta_l H_i^l \rightarrow 0 \quad \text{in} \quad L^2(Q_T).$$

The first three convergence relations imply

$$w_i^l := u_i^l + v_i^l \rightarrow \frac{1}{2n} \rho \quad \text{in} \quad L^2(Q_T).$$

Let $\alpha : \mathbb{R} \times \mathbb{R} \times Q \rightarrow \mathbb{R}$ be given by

$$\alpha(s, r, \mathbf{x}) := sf(s, \mathbf{x}) - (r - s)g(r - s, \mathbf{x}).$$

Then,

$$\begin{aligned} \left| \alpha(u_i^l, \frac{\rho}{2n}, \mathbf{x}) \right| &= \left| u_i^l f\left(u_i^l, \mathbf{x}\right) - \left(\frac{\rho}{2n} - u_i^l\right) g\left(\frac{\rho}{2n} - u_i^l, \mathbf{x}\right) \right| \\ &\leq \delta_l |H_i^l| + \left| \left(\frac{\rho}{2n} - u_i^l\right) g\left(\frac{\rho}{2n} - u_i^l, \mathbf{x}\right) - (w_i^l - u_i^l) g\left(w_i^l - u_i^l, \mathbf{x}\right) \right| \\ &\leq \delta_l |H_i^l| + M \left| \frac{\rho}{2n} - w_i^l \right|, \end{aligned}$$

which converges to zero in $L^2(Q_T)$ as $l \rightarrow \infty$. Moreover,

$$2M^{-1} \left| u_i^l - u_i^m \right| \leq \left| \alpha(u_i^l, \frac{\rho}{2n}, \mathbf{x}) - \alpha(u_i^m, \frac{\rho}{2n}, \mathbf{x}) \right| \leq 2M \left| u_i^l - u_i^m \right|,$$

which implies $\{u_i^l\}$ is a cauchy sequence in $L^2(Q_T)$. Therefore, the convergence of $|u_i^l - u_j^l| \rightarrow 0$ in $L^2(Q_T)$ implies that there is $u \in L^2(Q_T)$ such that

$$u_i^l \rightarrow \frac{u}{2n} \quad \text{in} \quad L^2(Q_T) \quad \text{as} \quad l \rightarrow \infty \quad \text{and} \quad \alpha\left(\frac{u}{2n}, \frac{\rho}{2n}, \mathbf{x}\right) = 0.$$

Finally, let's denote $v := \rho - u$ and see $v_i^l = w_i^l - u_i^l \rightarrow \frac{\rho - u}{2n} = \frac{v}{2n}$ in $L^2(Q_T)$. The last equation of the proposition follows from $\alpha\left(\frac{u}{2n}, \frac{\rho}{2n}, \mathbf{x}\right) = 0$. \square

6. DIFFUSION EQUATIONS

We have shown that $\rho^l = u^l + v^l \rightarrow \rho$, $u^l \rightarrow u$, and $v^l \rightarrow v$ in $L^2(Q_T)$ with $f(u/2n, \mathbf{x})u/2n = g(v/2n, \mathbf{x})v/2n$. In this section, we find diffusion equations satisfied by the total population $\rho = \lim_{l \rightarrow \infty} \sum_{i=1 \pm}^{n \pm} (u_i^l + v_i^l)$. The convergence of ρ^l , $\mathbf{J}^{u,l}$ and $\mathbf{J}^{v,l}$ as $l \rightarrow \infty$ together with (22) implies that

$$(24) \quad \partial_t \rho + \nabla \cdot (\mathbf{J}^u + \mathbf{J}^v) = 0$$

in the distribution sense. We split the case into two. First, let $\lim_{l \rightarrow \infty} \varepsilon_l / \delta_l = \ell \in [0, \infty)$, which covers the cases of Theorem 2.3 (i) and (ii). From (23), the following equations are satisfied in the distribution sense:

$$(25) \quad \begin{cases} \partial_k u / n = -\omega_u J_k^u + \ell(H_{k-} - H_{k+}), \\ \partial_k v / n = -\omega_v J_k^v - \ell(H_{k-} - H_{k+}). \end{cases}$$

We denote $f(u/2n, \mathbf{x})$, $g(v/2n, \mathbf{x})$, $\tilde{f}(u/2n, \mathbf{x})$, and $\tilde{g}(v/2n, \mathbf{x})$ by f , g , \tilde{f} , and \tilde{g} , respectively, for brevity. Since any two of $\{u, v, \rho\}$ are decided by any one of them, the four frequencies can be considered as a function of ρ after appropriate compositions.

Lemma 6.1. *Let $\lim_{l \rightarrow \infty} \varepsilon_l / \delta_l = \ell$. Then, for $i, j = 1\pm, \dots, n\pm$,*

$$H_i - H_j = \ell(J_{i,j}^u \tilde{f} - J_{i,j}^v \tilde{g}).$$

Proof. Consider the relation,

$$(26) \quad \begin{aligned} H_i^l - H_j^l &= \frac{f(u_i^l, \mathbf{x})u_i^l - f(u_j^l, \mathbf{x})u_j^l}{\delta_l} - \frac{g(v_i^l, \mathbf{x})v_i^l - g(v_j^l, \mathbf{x})v_j^l}{\delta_l} \\ &= \frac{f(u_i^l, \mathbf{x})u_i^l - f(u_j^l, \mathbf{x})u_j^l}{u_i^l - u_j^l} \frac{u_i^l - u_j^l}{\varepsilon_l} \frac{\varepsilon_l}{\delta_l} - \frac{g(v_i^l, \mathbf{x})v_i^l - g(v_j^l, \mathbf{x})v_j^l}{v_i^l - v_j^l} \frac{v_i^l - v_j^l}{\varepsilon_l} \frac{\varepsilon_l}{\delta_l}. \end{aligned}$$

The convergence of $u_i^l, v_i^l, J_{i,j}^{u,l}$ and $J_{i,j}^{v,l}$, the mean value theorem, and $\lim_{l \rightarrow \infty} \varepsilon_l / \delta_l = \ell$ implies that

$$H_i^l - H_j^l \rightarrow H_i - H_j = \ell(J_{i,j}^u \tilde{f} - J_{i,j}^v \tilde{g}).$$

□

Next we derive equations satisfied by the limit of the total population ρ . By plugging the relation of the lemma into (25) with $i = k-$ and $j = k+$, we obtain

$$\begin{cases} -J_k^u(\omega_u + \ell^2 \tilde{f}) + J_k^v \ell^2 \tilde{g} = \frac{1}{n} \partial_k u, \\ -J_k^v(\omega_v + \ell^2 \tilde{g}) + J_k^u \ell^2 \tilde{f} = \frac{1}{n} \partial_k v. \end{cases}$$

Now, by plugging them into (24), we can express J_k^u and J_k^v in terms of other terms above and obtain

$$(27) \quad \partial_t \rho = \frac{1}{n} \nabla \cdot \left(\frac{\ell^2(\tilde{f} + \tilde{g}) + \omega_v}{\omega_u \omega_v + \ell^2(\omega_u \tilde{g} + \omega_v \tilde{f})} \nabla u + \frac{\ell^2(\tilde{f} + \tilde{g}) + \omega_u}{\omega_u \omega_v + \ell^2(\omega_u \tilde{g} + \omega_v \tilde{f})} \nabla v \right).$$

We have

$$u = \frac{g}{f+g} \rho \quad \text{and} \quad v = \frac{f}{f+g} \rho$$

by Proposition 5.4. Plug them into (27), which directly gives (13) when $\ell = 0$. If $\ell \neq 0$, we can separate it into Fickian and Fokker-Planck parts as given in (14).

Finally, we consider the other case of Theorem 2.3(iii) when $\lim_{l \rightarrow \infty} \varepsilon_l / \delta_l = \infty$. By similarly rearranging terms as done in (26), we get

$$\frac{\delta_l}{\varepsilon_l} (H_i^l - H_j^l) \rightarrow (J_{i,j}^u \tilde{f} - J_{i,j}^v \tilde{g}) = 0.$$

The last equality is from L^2 boundedness of H_i^l on each Q_T and $\lim_{l \rightarrow \infty} \delta_l / \varepsilon_l = 0$. Therefore,

$$J_{i,j}^u = \frac{\tilde{g}}{\tilde{f} + \tilde{g}} J_{i,j} \quad \text{and} \quad J_{i,j}^v = \frac{\tilde{f}}{\tilde{f} + \tilde{g}} J_{i,j}.$$

After adding the two equations in (23) and then taking $l \rightarrow \infty$, we obtain

$$(28) \quad \frac{1}{n} \partial_k \rho = -\omega_u J_k^u - \omega_v J_k^v = -\frac{\tilde{\gamma}^{-1}(\rho, \mathbf{x})}{n} J_k.$$

The diffusion equation (15), $\rho_t = \nabla \cdot (\tilde{\gamma}(\rho, \mathbf{x}) \nabla \rho)$, comes from (24) and (28).

The next step is to identify the initial value of ρ . Using (22), we have

$$\int_0^\infty \int_Q \rho^l \partial_t \phi + \langle \mathbf{J}^l, \nabla \phi \rangle dx dt + \int \sum_{i=1\pm}^{n\pm} [u_{i,0}^l + v_{i,0}^l] \phi dx = 0$$

for all $\phi \in C^\infty(Q_\infty)$, which is periodic in \mathbf{x} and vanishes on $t > T$ for some $T > 0$. By taking $l \rightarrow \infty$, we have

$$\int_0^\infty \int_Q \rho \partial_t \phi + \langle \mathbf{J}, \nabla \phi \rangle dx dt + \int \sum_{i=1^\pm}^{n^\pm} [u_{i,0} + v_{i,0}] \phi dx = 0,$$

where $\mathbf{J} \in [L^2(Q_T)]^n$ and

$$\mathbf{J} = \begin{cases} -\nabla(\gamma(\rho, \mathbf{x})\rho) & \text{if } \varepsilon_l/\delta_l \rightarrow 0 \\ -\left(1 + \frac{\tilde{f}}{\omega_u} \ell^2 + \frac{\tilde{g}}{\omega_v} \ell^2\right)^{-1} \nabla(\gamma\rho) + \left(\frac{n\omega_u\omega_v}{(\tilde{f} + \tilde{g})\ell^2} + \frac{1}{\tilde{\gamma}}\right)^{-1} \nabla\rho & \text{if } \varepsilon_l/\delta_l \rightarrow \ell \\ -\tilde{\gamma}(\rho, \mathbf{x})\nabla\rho & \text{if } \varepsilon_l/\delta_l \rightarrow \infty. \end{cases}$$

The above implies that ρ is a weak solution of parabolic equations (13), (14), and (15), respectively, with initial value $\sum_{i=1^\pm}^{n^\pm} [u_{i,0} + v_{i,0}]$.

Remark 6.2 (Convergence). *By Proposition 7.2, which will be proved in the next section, we have $\gamma(\rho, \mathbf{x})\rho$ is C^2 , $\frac{1}{n\omega_u} \leq \partial_\rho(\gamma(\rho, \mathbf{x})\rho) \leq \frac{1}{n\omega_v}$, and $|\nabla_{\mathbf{x}}(\gamma(\rho, \mathbf{x})\rho)| \leq M\rho$ for some $M > 0$ if $\tau f(\tau, \mathbf{x})$ and $\tau g(\tau, \mathbf{x})$ are C^2 and admissible. From standard theories for uniformly parabolic equations of divergence type, each of the three cases, (13), (14), and (15), has a unique weak solution when the periodic boundary condition and initial value are imposed. This uniqueness implies that the subsequential convergence of $\{u^h, v^h\}$ is actually the convergence.*

7. CHARACTERIZATION OF THE MOTILITY FUNCTION

The diffusion equations in Theorem 2.3 are obtained when turning frequencies, ω_u and ω_v , and state transition frequencies, f and g , are given. The motility function γ depends on these parameter functions. The remaining question is the existence of such parameters that produce a given motility function γ . We first obtain a regularity and a gradient estimate of $\rho\gamma(\rho, \mathbf{x})$ when transition frequencies f and g are admissible. Then, we will see that the obtained regularity properties are sufficient conditions to obtain admissible transition frequencies f and g that produce the same motility function γ . In the second part of the section, we show that starvation driven diffusion is obtained as a diffusive limit.

7.1. Characterization of γ . We consider the regularity relation among u, v, ρ, γ and $\tilde{\gamma}$. If ρ is given, we can find u and v implicitly by the two relations in (29). The regularity of f and g is naturally conveyed to others by the implicit function theorem. We often consider ρ as an independent variable. Then, u and v are functions of ρ and \mathbf{x} .

Lemma 7.1. *Let $\alpha : \mathbb{R} \times \mathbb{R} \times Q \rightarrow \mathbb{R}$ be given by*

$$\alpha(s, r, \mathbf{x}) := sf(s, \mathbf{x}) - (r - s)g(r - s, \mathbf{x}),$$

where the odd extension of $\tau f(\tau, \mathbf{x})$ and $\tau g(\tau, \mathbf{x})$ in Remark 2.2 is taken. Then, for each $(r, \mathbf{x}) \in \mathbb{R}^+ \times Q$, there is a unique $s = s(r, \mathbf{x}) \in [0, r]$ such that

$$\alpha(s(r, \mathbf{x}), r, \mathbf{x}) = 0,$$

and $s(r, \mathbf{x})$ is in $C^k(\mathbb{R}^+ \times Q)$ if $\tau f(\tau, \mathbf{x})$ and $\tau g(\tau, \mathbf{x})$ are in $C^k(\mathbb{R}^+ \times Q)$ for some $k \geq 1$.

Proof. By (2) of Definition 2.1, $\frac{\partial \alpha}{\partial s} \geq \frac{2}{M} > 0$. Unique existence of $s(r, \mathbf{x})$ for each (r, \mathbf{x}) follows from the intermediate value theorem. We conclude the function $s(r, \mathbf{x})$ is in $C^k([0, \infty) \times Q)$ by the implicit function theorem. \square

Proposition 7.2. *Let f and g be admissible frequencies, $\tau f(\tau, \mathbf{x})$ and $\tau g(\tau, \mathbf{x})$ be $C^k(\mathbb{R}^+ \times Q)$ for $k \geq 1$, and $u = u(\rho, \mathbf{x})$ and $v = v(\rho, \mathbf{x})$ be defined by two relations,*

$$(29) \quad u + v = \rho \quad \text{and} \quad \frac{u}{2n} f\left(\frac{u}{2n}, \mathbf{x}\right) = \frac{v}{2n} g\left(\frac{v}{2n}, \mathbf{x}\right).$$

Then, u and v are in $C^k([0, \infty) \times Q)$,

$$\tilde{\gamma}(\rho, \mathbf{x}) \in C^{k-1}([0, \infty) \times Q), \quad \gamma(\rho, \mathbf{x})\rho \in C^k([0, \infty) \times Q),$$

$$\frac{1}{n\omega_u}(1 + \varepsilon) \leq \tilde{\gamma}(\rho, \mathbf{x}), \quad \partial_\rho(\gamma(\rho, \mathbf{x})\rho) \leq \frac{1}{n\omega_v}(1 - \varepsilon) \quad \text{for some } \varepsilon > 0,$$

and

$$|\nabla_{\mathbf{x}}\gamma(\rho, \mathbf{x})\rho| \leq \tilde{M}\rho \quad \text{for some } \tilde{M} > 0.$$

Proof. The first part of the proposition comes from Lemma 7.1 if we choose

$$u(\rho, \mathbf{x}) = 2ns(\rho/2n, \mathbf{x}) \quad \text{and} \quad v(\rho, \mathbf{x}) = \rho - u(\rho, \mathbf{x}),$$

where $s(\rho/2n, \mathbf{x})$ is the one in Lemma 7.1. Since $\tau f(\tau, \mathbf{x})$, $\tau g(\tau, \mathbf{x}) \in C^k([0, \infty) \times Q)$, we have

$$\tilde{f}(\tau, \mathbf{x}), \quad \tilde{g}(\tau, \mathbf{x}) \in C^{k-1}([0, \infty) \times Q).$$

Thus, the regularity of u , v , \tilde{f} , and \tilde{g} implies that $\tilde{\gamma}(\rho, \mathbf{x})$ in (11) is $C^{k-1}([0, \infty) \times Q)$ since it is a composition of C^k and C^{k-1} functions. Upper and lower bounds of $\tilde{\gamma}$ is from the ones of \tilde{f} and \tilde{g} .

Observe that $\frac{f(u/2n, \mathbf{x})}{f(u/2n, \mathbf{x}) + g(v/2n, \mathbf{x})}\rho = v(\rho, \mathbf{x}) \in C^k([0, \infty) \times Q)$. Therefore, γ in (11) satisfies

$$\gamma(\rho, \mathbf{x})\rho = \frac{1}{n} \left[\frac{1}{\omega_u}(\rho - v(\rho, \mathbf{x})) + \frac{1}{\omega_v}v(\rho, \mathbf{x}) \right] \in C^k([0, \infty) \times Q).$$

By differentiating the implicit relation,

$$(30) \quad \frac{\rho - v}{2n} f\left(\frac{\rho - v}{2n}, \mathbf{x}\right) - \frac{v}{2n} g\left(\frac{v}{2n}, \mathbf{x}\right) = 0,$$

with respect to ρ , we obtain

$$\frac{1}{M^2 + 1} \leq \frac{\partial v}{\partial \rho} = \frac{\partial_\tau(\tau \hat{f}(\tau, \mathbf{x}))|_{\tau=u/2n}}{\partial_\tau(\tau \hat{f}(\tau, \mathbf{x}))|_{\tau=u/2n} + \partial_\tau(\tau \hat{g}(\tau, \mathbf{x}))|_{\tau=v/2n}} \leq \frac{M^2}{M^2 + 1}.$$

Therefore, the upper bound for $\partial_\rho(\gamma(\rho, \mathbf{x})\rho)$ immediately follows. If we differentiate (30) with respect to \mathbf{x} with a fixed ρ , we obtain

$$\begin{aligned} & \left[\frac{\partial}{\partial \tau}(\tau \hat{f}(\tau, \mathbf{x})) \Big|_{\tau=\frac{\rho-v}{2n}} + \frac{\partial}{\partial \tau}(\tau \hat{g}(\tau, \mathbf{x})) \Big|_{\tau=\frac{v}{2n}} \right] \nabla_{\mathbf{x}} v \\ &= \nabla_{\mathbf{x}} \left[\frac{\rho - v}{2n} f\left(\frac{\rho - v}{2n}, \mathbf{x}\right) - \frac{v}{2n} g\left(\frac{v}{2n}, \mathbf{x}\right) \right]. \end{aligned}$$

This implies that

$$|\nabla_{\mathbf{x}} v| \leq \frac{M}{2} \left[M \frac{u}{2n} + M \frac{v}{2n} \right] = \frac{M^2}{4n} \rho.$$

Since $\nabla_{\mathbf{x}} \rho \gamma(\rho, \mathbf{x}) = \frac{1}{n} \left(\frac{1}{\omega_u} - \frac{1}{\omega_v} \right) \nabla_{\mathbf{x}} v$, the last estimate of the proposition follows. \square

We now consider the existence of state transition frequencies for a given γ . For a simpler presentation, we write it in terms of $v(\rho, \mathbf{x})$ and ρ is considered as an independent variable in the following proposition. First, consider an elementary lemma.

Lemma 7.3. *Let a function r be $C^k([0, \infty))$ for $k \geq 1$ with $r(0) = 0$. Then,*

$$\frac{r(x)}{x} \in C^{k-1}([0, \infty))$$

and

$$\left(\frac{r(x)}{x}\right)^{(k)} = o\left(\frac{1}{x}\right) \text{ as } x \rightarrow 0^+.$$

Proof. Note that $r(x)/x$ is already in $C^k((0, \infty))$. For $x > 0$ and $0 \leq h \leq k$,

$$\left(\frac{r(x)}{x}\right)^{(h)} = \frac{(-1)^h h!}{x^{h+1}} \left[\sum_{i=0}^h (-x)^i \frac{r^{(i)}(x)}{i!} \right].$$

For $0 \leq h < k$, L'hospital's rule gives

$$\begin{aligned} \lim_{x \rightarrow 0^+} \left(\frac{r(x)}{x}\right)^{(h)} &= \lim_{x \rightarrow 0^+} \frac{(-1)^h h! \left[\sum_{i=0}^h (-x)^i \frac{r^{(i)}(x)}{i!} \right]}{x^{h+1}} \\ &= \lim_{x \rightarrow 0^+} \frac{(-1)^h h! \left[(-x)^h \frac{r^{(h+1)}(x)}{h!} \right]}{(h+1)x^h} = \frac{r^{(h+1)}(0)}{h+1}. \end{aligned}$$

Therefore, $\frac{r(x)}{x} \in C^h([0, \infty))$ for $0 \leq h < k$. Similar argument based on L'hospital's rule leads to

$$\lim_{x \rightarrow 0^+} x \left(\frac{r(x)}{x}\right)^{(k)} = 0.$$

□

Proposition 7.4. *Let $0 < \omega_v < \omega_u$, $u(\rho, \mathbf{x}) \in C^1([0, \infty) \times Q)$ and $\gamma(\rho, \mathbf{x})\rho \in C^1([0, \infty) \times Q)$ satisfy periodic boundary condition in $\mathbf{x} \in Q$, and*

$$\gamma(\rho, \mathbf{x})\rho = \frac{1}{n} \left[\frac{1}{\omega_u} u(\rho, \mathbf{x}) + \frac{1}{\omega_v} (\rho - u(\rho, \mathbf{x})) \right].$$

Suppose that there exist ε and $M > 0$ such that

- (1) $\varepsilon \leq \partial_\rho u(\rho, \mathbf{x}) \leq 1 - \varepsilon$,
- (2) $\|\nabla_{\mathbf{x}} u(\rho, \mathbf{x})\| \leq M\rho$.

Then, there exist a pair of admissible transition frequencies f and g which satisfy

$$\frac{u}{2n} f\left(\frac{u}{2n}, \mathbf{x}\right) = \frac{\rho - u}{2n} g\left(\frac{\rho - u}{2n}, \mathbf{x}\right),$$

and a normalization condition

$$f\left(\frac{u}{2n}, \mathbf{x}\right) + g\left(\frac{\rho - u}{2n}, \mathbf{x}\right) = 1$$

for all $(\rho, \mathbf{x}) \in \mathbb{R}_+ \times Q$. Under this normalization condition, $f(\tau, \mathbf{x})$ and $g(\tau, \mathbf{x})$ are uniquely decided for all $\tau > 0$.

Proof. We consider existence and the admissibility conditions for $\tau f(\tau, \mathbf{x})$. Similar arguments give the same result for $\tau g(\tau, \mathbf{x})$. During the proof, we may set

$$(31) \quad v = v(\rho, \mathbf{x}) = \rho - u(\rho, \mathbf{x}).$$

First, the condition (1) and the inverse function theorem implies $(u, \mathbf{x}) \mapsto (\rho, \mathbf{x})$ is C^1 on $[0, \infty) \times Q$ and vice versa. Moreover, for $u \neq 0$, conditions imply

$$\frac{u}{2n} f\left(\frac{u}{2n}, \mathbf{x}\right) = \frac{u}{2n\rho} v(\rho, \mathbf{x}) = \frac{u}{2n\rho} (\rho - u) = \frac{u}{2n} \left(1 - \frac{u}{\rho}\right).$$

By using the relation $\rho = \rho(u, \mathbf{x})$, the above equation is written as

$$(32) \quad \tau f(\tau, \mathbf{x}) = \tau \left(1 - \frac{2n\tau}{\rho(2n\tau, \mathbf{x})} \right).$$

This explicit expression gives the uniqueness of such $\tau f(\tau, \mathbf{x})$. By Lemma 7.3 applied to $u(\rho, \mathbf{x}) \left(\frac{u(\rho, \mathbf{x})}{\rho} \right)$, we have

$$A(\rho, \mathbf{x}) := \frac{u(\rho, \mathbf{x})}{2n} \left(1 - \frac{u(\rho, \mathbf{x})}{\rho} \right) \in C^1([0, \infty) \times Q).$$

Therefore,

$$\tau f(\tau, \mathbf{x}) = A(\rho(2n\tau, \mathbf{x}), \mathbf{x}) \in C^1([0, \infty) \times Q).$$

It remains to show admissibility conditions of $\tau f(\tau, \mathbf{x})$. From (32), for $\tau > 0$,

$$\begin{aligned} \partial_\tau(\tau f(\tau, \mathbf{x})) &= 1 - 2\frac{2n\tau}{\rho} + \frac{(2n\tau)^2}{\rho^2}(\partial_u \rho) \\ &= \left(1 - \frac{u}{\rho} \right)^2 + \frac{u^2}{\rho^2} \left(\frac{1}{\partial_\rho u} - 1 \right). \end{aligned}$$

Since $\varepsilon \leq \partial_\rho u = \partial_\rho(\rho - v)$, $\frac{u}{\rho}$, $(1 - \frac{u}{\rho}) \leq 1 - \varepsilon$, we have

$$\begin{aligned} \frac{\varepsilon^2}{1 - \varepsilon} &= \varepsilon^2 + \varepsilon^2((1 - \varepsilon)^{-1} - 1) \\ &\leq \partial_\tau(\tau f(\tau, \mathbf{x})) \leq (1 - \varepsilon)^2 + (1 - \varepsilon)^2(\varepsilon^{-1} - 1) = \frac{(1 - \varepsilon)^2}{\varepsilon}, \end{aligned}$$

and the first admissibility condition is obtained.

Finally, from (32),

$$\nabla_{\mathbf{x}}(\tau f(\tau, \mathbf{x})) = \frac{2n\tau^2}{\rho^2} \nabla_{\mathbf{x}} \rho.$$

Taking derivative of $u(\rho(\tau, \mathbf{x}), \mathbf{x}) = \tau$ with respect to \mathbf{x} , we get

$$\nabla_{\mathbf{x}} u + \partial_\rho u \nabla_{\mathbf{x}} \rho = 0$$

and hence

$$|\nabla_{\mathbf{x}} \rho| \leq \frac{|\nabla_{\mathbf{x}} u|}{\partial_\rho u} \leq \frac{M}{\varepsilon} \rho.$$

Therefore,

$$|\nabla_{\mathbf{x}}(\tau f(\tau, \mathbf{x}))| \leq \frac{2n\tau^2}{\rho^2} \|\nabla_{\mathbf{x}} \rho\| \leq \frac{u}{\rho\varepsilon} \tau M \leq \frac{1 - \varepsilon}{\varepsilon} \tau M.$$

□

7.2. Application to starvation driven diffusion. In the context of starvation driven diffusion, we may take γ as a departing probability depending on the environment. If starvation started, the species increases the departing probability and the corresponding situation can be modeled by a Fokker-Planck type diffusion equation,

$$(33) \quad \rho_t = \Delta(\gamma(s)\rho),$$

where the quantity s measures the intensity of starvation and γ is an increasing function of s , i.e.,

$$\gamma'(s) \geq 0.$$

We may ask if there exist a pair of transition frequencies f and g which are functions of the starvation measure s and produce the same diffusion equation as the diffusion limit. In this way we may justify the classical idea of heterogeneous departing probability in terms of microscopic individual dynamics.

From the characterization of γ shown previously, we know when there exist a pair of transition frequencies $f(\tau, \mathbf{x})$ and $g(\tau, \mathbf{x})$ which produce a given starvation driven diffusion in Fokker-Planck type such as (13). Moreover, we will see in a moment that such SDD equations are obtained by choosing transition frequencies as functions of fractional starvation measures, i.e.,

$$f(\tau, \mathbf{x}) = f\left(\frac{\tau}{m(\mathbf{x})}\right) \quad \text{and} \quad g(\tau, \mathbf{x}) = g\left(\frac{\tau}{m(\mathbf{x})}\right).$$

The proof is quite straightforward. In the limit, by Theorem 2.3, the transition frequencies f and g are functions of the starvation measures

$$s_u = \frac{u(\rho, \mathbf{x})}{2n m(\mathbf{x})} \quad \text{and} \quad s_v = \frac{v(\rho, \mathbf{x})}{2n m(\mathbf{x})}, \quad \text{respectively,}$$

and the ratio between s_u and s_v are determined by

$$s_u f(s_u) = s_v g(s_v).$$

Therefore, if any one of s_u , s_v and s is given, the others are determined. Thus, the motility γ in (11) is a function of the starvation measure

$$s = s_u + s_v = \frac{\rho}{2n m(\mathbf{x})}.$$

Theorem 7.5. *Suppose that $\gamma(s)$ and $m(\mathbf{x})$ are C^1 , bounded, and bounded away from zero. Furthermore, assume that $\|\nabla_{\mathbf{x}} m\|$ and $s\gamma'(s)$ are bounded, $m(\mathbf{x})$ is periodic, and $\gamma'(s) \geq 0$. Then, for each pair (ω_u, ω_v) such that*

$$(34) \quad \frac{1}{n\omega_u} + \varepsilon < (s\gamma(s))' = \gamma(s) + s\gamma'(s) < \frac{1}{n\omega_v} - \varepsilon \quad \text{for some } \varepsilon > 0,$$

there exists a unique pair of admissible transition frequencies such that $\tau f(\tau, \mathbf{x})$ and $\tau g(\tau, \mathbf{x})$ are in C^1 , the limit of the total population ρ in Theorem 2.3 satisfies (33) if $\varepsilon/\delta \rightarrow 0$, and

$$\left[f\left(\frac{u(\rho, \mathbf{x})}{2n}, \mathbf{x}\right) + g\left(\frac{v(\rho, \mathbf{x})}{2n}, \mathbf{x}\right) \right] = 1 \quad \text{for } \rho > 0.$$

Moreover, f and g are of a form

$$f(\tau, \mathbf{x}) = f(\tau/m(\mathbf{x})) \quad \text{and} \quad g(\tau, \mathbf{x}) = g(\tau/m(\mathbf{x}))$$

Proof. By regarding $\gamma(s)\rho$ as a function of (ρ, \mathbf{x}) ,

$$\partial_\rho \left[\gamma\left(\frac{\rho}{2nm(\mathbf{x})}\right) \rho \right] = \gamma\left(\frac{\rho}{2nm(\mathbf{x})}\right) + \gamma'\left(\frac{\rho}{2nm(\mathbf{x})}\right) \left(\frac{\rho}{2nm(\mathbf{x})}\right) = \partial_s(s\gamma(s))$$

and

$$\nabla_{\mathbf{x}} \left[\gamma\left(\frac{\rho}{2nm(\mathbf{x})}\right) \rho \right] = \gamma'(s)s \left(\frac{-\nabla_{\mathbf{x}} m(\mathbf{x})}{m(\mathbf{x})} \right) \rho$$

imply $\gamma(s)\rho$ satisfies assumptions of Proposition 7.4. Hence by the proposition, unique existence of f and g are known. We only need to prove the last statement. By writing

$$\gamma(s)s = \frac{1}{n} \left[\frac{1}{\omega_u} (1 - h(s))s + \frac{1}{\omega_v} h(s)s \right],$$

we notice

$$s_u = \frac{u(\rho, \mathbf{x})}{2nm(\mathbf{x})} = s(1 - h(s)) = sg\left(\frac{v(\rho, \mathbf{x})}{2n}, \mathbf{x}\right) = s \left(1 - f\left(\frac{u(\rho, \mathbf{x})}{2n}, \mathbf{x}\right) \right).$$

Since $\delta \leq (s(1 - h(s)))' \leq 1 - \delta$ for some $\delta > 0$, we have $\alpha(\cdot)$ which is the C^1 inverse function of $s(1 - h(s))$. Now for $\rho > 0$ and hence $u(\rho, \mathbf{x}) > 0$,

$$f\left(\frac{u(\rho, \mathbf{x})}{2n}, \mathbf{x}\right) = h(\alpha(s_u)) = h\left(\alpha\left(\frac{u(\rho, \mathbf{x})}{2nm(\mathbf{x})}\right)\right).$$

Therefore, $f(\tau, \mathbf{x}) = (h \circ \alpha)(\tau/m(\mathbf{x}))$ and similar results holds for g . \square

8. SUMMARY AND CONCLUSION

Diffusion is a macroscopic scale observation of microscopic scale random movement, which is one of the most widely observed transport phenomena. Diffusion limits of various kinetic models have been investigated to understand the connection between the two processes of different scales. The focus of this paper is in verifying biological diffusion models in spatially heterogeneous environment. There has been a long controversy in finding the correct diffusion. In particular, Fickian and Fokker-Planck type diffusions are often claimed as the correct one. The main contribution of this paper is to clarify the relation between the two models by deriving the both from a single kinetic system and provides insight what they are modeling for.

In this paper we have considered a mesoscopic scale discrete kinetic model (7)-(8) in the context of bacteria chemotaxis in n space dimensions (or (5) with $\eta = \varepsilon^2/\delta^2$ in 1-D). Note that there is no term biased by a chemical *gradient* which is usually taken to obtain a chemotactic term (see [31, 32]). Instead, there are two states of organisms, u and v , which tumble with different frequencies $\omega_v < \omega_u$. The population ratio of the two states depends on the spatially heterogeneous chemical (or food) distribution and is decided by transition frequencies. Finally, it is shown in Theorem 2.3 that, if $\varepsilon/\delta \rightarrow \ell$, the limit of the total population, $\rho = u + v$, satisfies the diffusion equation (14). This equation turns into Fokker-Planck or Fickian type diffusion equation as $\ell \rightarrow 0$ or $\ell \rightarrow \infty$, respectively.

The case of $\varepsilon/\delta \rightarrow 0$ ($\ell = 0$) is the one that the turning (or tumbling) mechanism is more frequent than the state transition one. In this case the spatial heterogeneity of the ratio of the two state produces Fokker-Planck type diffusion in (13). On the other hand, $\varepsilon/\delta \rightarrow \infty$ ($\ell = \infty$) is the case that there are a lot of state transitions between two consecutive turns. In this case the state of different turning frequencies loses its meaning and the Fickian diffusion is obtained. Hence, we conclude that the Fokker-Planck type diffusion is the meaningful biological diffusion in the context of the discrete kinetic system of the paper.

The main goal of the chemotaxis theory is to understand the advection phenomenon activated by nonuniform chemical distributions. Traditional kinetic models are biased by the chemical gradient and produce Fickian diffusion and advection separately. Those theories are based on the hypothesis that organisms can measure the chemical gradient. There are relatively less efforts to explain the phenomenon without such a hypothesis. Fokker-Planck type diffusion in an exact form such as (13) can be found from cross diffusion theory (see [15, 27]) or starvation driven diffusion theory([7]). Such a diffusion has been applied to chemotaxis models and has produced the traveling wave, the aggregation phenomena and global existence [9, 35, 36].

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APPENDIX A. LIST OF NOTATION USED IN THE PAPER

In this paper we are using the following notations:

- (1) Indices: $i, j \in \{1+, 1-, \dots, n+, n-\}$; $k, m, h, l \in \{1, 2, \dots\}$.
- (2) $\mathbf{e}_{k\pm} = \pm \mathbf{e}_k$ where $\{\mathbf{e}_k\}$ is the standard orthonormal basis of \mathbb{R}^n .
- (3) $u = \sum_{i=1\pm}^{n\pm} u_i$, $v = \sum_{i=1\pm}^{n\pm} v_i$.
- (4) $Q = [-1, 1]^n$, $Q_T = Q \times (0, T)$, $Q_\infty = Q \times (0, \infty)$, $\mathbb{R}^+ = [0, \infty)$.
- (5) $J_{i,j}^{u,\varepsilon} = \frac{u_i - u_j}{\varepsilon}$, $J_k^{u,\varepsilon} = J_{k+,k-}^{u,\varepsilon}$, $\mathbf{J}^{u,\varepsilon} = (J_1^{u,\varepsilon}, J_2^{u,\varepsilon}, \dots, J_n^{u,\varepsilon})$.

- (6) $J_{i,j}^{v,\varepsilon} = \frac{v_i - v_j}{\varepsilon}, J_k^{v,\varepsilon} = J_{k+,k-}^{v,\varepsilon}, \mathbf{J}^{v,\varepsilon} = (J_1^{v,\varepsilon}, J_2^{v,\varepsilon}, \dots, J_n^{v,\varepsilon}).$
(7) $J_{i,j}^{\rho,\varepsilon} = J_{i,j}^{u,\varepsilon} + J_{i,j}^{v,\varepsilon}, J_k^{\rho,\varepsilon} = J_k^{u,\varepsilon} + J_k^{v,\varepsilon}, \mathbf{J}^{\rho,\varepsilon} = \mathbf{J}^{u,\varepsilon} + \mathbf{J}^{v,\varepsilon}.$
(8) $H_i^\delta = \frac{f(u_i, \mathbf{x})u_i - g(v_i, \mathbf{x})v_i}{\delta}.$
(9) $\text{sign}^+(a) = \begin{cases} 1, & a > 0, \\ 0, & a \leq 0. \end{cases}$
(10) $\|\cdot\|$ denotes the uniform norm.

APPENDIX B. RELATION BETWEEN MICROSCOPIC AND MACROSCOPIC SCALES

The diffusion limit with a single phenotype group is well understood. Here we briefly introduce the scaling relation between the microscopic and macroscopic quantities and show how the diffusivity d_u of a species is related by microscopic scale quantities. Let u be the population density of the species. Using the random walk idea it is assumed that each individual moves to one of the $2n$ directions, $\pm \mathbf{e}_k, k = 1, \dots, n$, in n dimensional space with the unit speed in the microscopic scale. Denote $\mathbf{e}_{k\pm} = \pm \mathbf{e}_k$ and let u_i be the fractional population densities that moves to directions $\mathbf{e}_i, i = 1\pm, \dots, n\pm$. Then, we have

$$u = \sum_{i=1\pm}^{n\pm} u_i.$$

If the species changes the moving direction randomly with a rate ω_u , then the evolution of the population density is modeled by

$$\partial_s u_i + \mathbf{e}_k \cdot \nabla_{\mathbf{y}} u_i = \frac{\omega_u}{2n} \sum_{j=1}^n (u_{j+} + u_{j-}) - \omega_u u_i.$$

The time and space variables, s and \mathbf{y} , in the equation are of microscopic scale. Let $\varepsilon > 0$ be small and introduce variables in a macroscopic scale,

$$t = \varepsilon^2 s, \quad \mathbf{x} = \varepsilon \mathbf{y}.$$

Here, we have taken the scale of diffusion phenomenon. Then, after changing the variables, we obtain

$$\partial_t u_i + \frac{1}{\varepsilon} \mathbf{e}_k \cdot \nabla_{\mathbf{x}} u_i = \frac{1}{\varepsilon^2} \left(\frac{\omega_u}{2n} \sum_{j=1}^n (u_{j+} + u_{j-}) - \omega_u u_i \right).$$

Notice that solutions depend on the parameter $\varepsilon > 0$, i.e., $u = u^\varepsilon$, and the convergence $u^\varepsilon \rightarrow U$ as $\varepsilon \rightarrow 0$ has been understood well and the limit satisfies

$$\partial_t U = d_u \Delta U \quad \text{with} \quad d_u = \frac{1}{n\omega_u}.$$

If $f = 0$ and $v(0) = 0$, then $v(t) = 0$ for all $t \geq 0$ and hence the system (7)-(8) is identical to the above. In the case, γ in (11) is $\gamma = \frac{1}{n\omega_u}$. Therefore, the equation (13) is written as

$$u_t = \frac{1}{n\omega_u} \Delta u,$$

which is identical to the single phenotype case.

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