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Fluid and diffusion limits for the Poisson encounter-mating model

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ABSTRACT. Stochastic encounter-mating (SEM) models describe monogamous permanent pair formation in finite zoological populations of multitype females and males. In this article we study SEM with Poisson firing times. We prove that an infinite population corresponds to a fluid limit, i.e., the stochastic dynamics converges to a deterministic system governed by coupled ODEs. Moreover, we establish a functional central limit theorem and give a diffusion approximation for the model. Next, we convert the fluid limit ODEs to the well-known Lotka-Volterra and replicator equations from population dynamics. Under the so-called fine balance condition, which characterizes panmixia for finite populations, we solve the corresponding replicator equations and give an exact expression for the fluid limit. Finally, we consider the case with two types of females and males. Without the fine balance assumption, but under some symmetry conditions, we give an explicit formula for the limiting mating pattern, and then use it to fully characterize assortative mating.

1. INTRODUCTION

1.1. **The model.** Consider a zoological population consisting of n females and n males, divided into k types which are labeled $1, \ldots, k$. We denote by $x_i^{(n)} \geq 0$ the number of type-i females and by $y_j^{(n)} \geq 0$ the number of type-j males, for $i, j \in [k] := \{1, \ldots, k\}$. To each type-$i$ female (resp. type-j male) a Poisson process with rate α_i (resp. β_j) is attached. These Poisson processes are mutually independent and are called firing times. Consider a $k \times k$ matrix $P = (p_{ij})_{i,j \in [k]}$, with $0 < p_{ij} \leq 1$, which we refer to as mating preferences. The dynamics is described as follows. Start with a population of only singles. At any time, when the Poisson clock of one of the single individuals rings (by the Poisson assumption no two individuals' clocks ring at the same time), it chooses a single individual from the opposite sex, uniformly at random, to form a temporary pair. Next, if this temporary pair is comprised of a type-i female and a type-j male, it becomes a permanent pair with probability p_{ij} and the individuals in that pair leave the singles pool; otherwise the temporary pair is broken and the individuals go back to the singles pool. We refer to this two-stage permanent pair formation model as Poisson encounter-mating (Poisson EM). Observe that the number of types present in the female and male populations need not be the same, setting, e.g., $x_i^{(n)} = 0$ would take type-i females out of the picture. Hence, there can be an unequal number of female and male types, however, the setup above is notationally convenient.

We designate by $Q_{ij}^{(n)}(t), \ t \geq 0$, the number of type-$ij$ pairs at time t. Here, the first index always refers to the female type and the second to the male type. We call the $k \times k$ matrix valued process $Q^{(n)}(t) = (Q_{ij}^{(n)}(t))_{i,j \in [k]}$ the pair-type process. Since the Poisson processes are memoryless, $Q^{(n)}$ is a pure jump continuous-time Markov process. In order to formally define $Q^{(n)}$ we briefly introduce some notation. Let $\mathcal{M}^{k \times k}(A)$ denote the set of $k \times k$ matrices whose entries are in $A \subseteq \mathbb{R}$. For $M = (M_{ij})_{i,j \in [k]} \in \mathcal{M}^{k \times k}(A)$ we define the i-th row sum, the j-th column sum and the grand total of M, respectively, via

$$M_{i,\cdot} = \sum_{j'=1}^{k} M_{ij'}, \quad M_{\cdot,j} = \sum_{i'=1}^{k} M_{i'j}, \quad M_{tot} = \sum_{i'=1}^{k} \sum_{j'=1}^{k} M_{i'j'}.$$

We denote by I^{ij} the $k \times k$ matrix whose entries are zero except the ij-th entry, which is one. Throughout this article we use the max norm on $\mathcal{M}^{k \times k}(A)$ given by $|M| = \max_{i,j \in [k]} |M_{ij}|$. Since all matrix norms are equivalent, our results are valid for any choice of norm.

The pair-type process $Q^{(n)}$ is a continuous-time Markov process taking values in $\mathcal{M}^{k \times k}(\mathbb{N} \cup \{0\})$ that has jumps of size 1, more precisely, the transitions are from M to $M + I^{ij}$ for $i, j \in [k]$. The transition rates are given by

$$(1.1) \qquad \rho(M, M + I^{ij}) = \frac{\pi_{ij}\left(x_i^{(n)} - M_{i,\cdot}\right)\left(y_j^{(n)} - M_{\cdot,j}\right)}{n - M_{tot}}$$

where
$$\Pi = (\pi_{ij})_{i,j \in [k]}, \quad \pi_{ij} = p_{ij}(\alpha_i + \beta_j),$$
with the convention that $\rho(M, \cdot) \equiv 0$ for M with $M_{tot} = n$.

Let us explain the formula in (1.1). When the pair-type formation at a time is M, the number of type-i females (resp. type-j males) in the singles pool is $x_i^{(n)} - M_{i,\cdot}$ (resp. $y_j^{(n)} - M_{\cdot,j}$). Also, by the description of the model, the total number of single females is always equal to that of males and given by $n - M_{tot}$. A new type-ij pair is formed in two ways: either the clock of a type-i single female rings, this female encounters a type-j single male to form a temporary pair, and finally, this pair becomes permanent; or similar has to happen with a type-j single male's clock ringing. In the first scenario, the total rate with which the clock of a type-i single female rings is $\alpha_i(x_i^{(n)} - M_{i,\cdot})$, the probability that it samples a type-j male from single males is $(y_j^{(n)} - M_{\cdot,j})/(n - M_{tot})$, the probability that the temporary pair formed becomes permanent is p_{ij}, and the product of these terms gives the rate of this event. The corresponding terms in the second scenario are $\beta_j(y_j^{(n)} - M_{\cdot,j})$, $(x_i^{(n)} - M_{i,\cdot})/(n - M_{tot})$ and p_{ij}. Finally, the sum of the rates of these two events gives (1.1).

Since $Q^{(n)}$ is a pure jump Markov process for all n, it is possible to define the whole family $\{Q^{(n)} : n \in \mathbb{N}\}$ via a collection of independent standard Poisson processes whose joint distribution we denote by $\mathbb{P}$ (see Section 2). Since we are interested in the infinite population asymptotics, we assume that there are non-negative numbers $x_1, \ldots, x_k$ and $y_1, \ldots, y_k$ such that for all $i, j \in [k]$, as $n \to \infty$

(1.2)
$$\frac{x_i^{(n)}}{n} \longrightarrow x_i, \quad \frac{y_j^{(n)}}{n} \longrightarrow y_j.$$

Note that $x_1 + \cdots + x_k = y_1 + \cdots + y_k = 1$. We refer to such a collection of numbers $x_1, \ldots, x_k$, $y_1, \ldots, y_k$ as an infinite population of the species.

The pair-type process $Q^{(n)}$ naturally stops at
$$T_n := \inf\{t \geq 0 : Q_{tot}^{(n)}(t) = n\},$$
that is, when the singles pool is depleted and every individual is in a permanent pair. $Q^{(n)}(T_n)$ is called the mating pattern of the population and is of central importance in this paper. Note that $Q^{(n)}(T_n)$ is a random $k \times k$ matrix (or a contingency table) whose i-th row sum is $x_i^{(n)}$ and j-th column sum is $y_j^{(n)}$ for all $i, j \in [k]$. We always assume that $p_{ij} > 0$ and $\alpha_i + \beta_j > 0$ for all $i, j \in [k]$. Hence, almost surely $T_n < \infty$.

One fundamental question about the mating pattern is whether correlations exist between female and male types. Zero correlations correspond to the case where the frequency of type-ij pair is given by the product of the frequencies of type-i females and type-j males and has been called "panmixia"in the literature. Since we investigate Poisson EM as the population size diverges and establish almost sure limit theorems for the normalized mating pattern $Q^{(n)}(T_n)/n$, we naturally use the following definition of panmixia.

DEFINITION 1.1. *The species is said to be panmictic if $\mathbb{P}$-a.s.*
$$\lim_{n \to \infty} \frac{Q_{ij}^{(n)}(T_n)}{n} = x_i y_j, \qquad \forall i, j \in [k],$$
for any infinite population $x_1, \ldots, x_k, y_1, \ldots, y_k$.

Complementing the concept of panmixia is assortative mating. Homogamy (resp. heterogamy) describes the situations where there are positive (resp. negative) correlations in the mating pattern between females and males with similar types. To make the definition of assortative mating precise one needs a (genotypical or phenotypical) distance on the space of types. Such a structure for types must

be reflected on preferences and this requires a more complex model. However, when $k = 2$, we can conveniently define assortative mating since there is a unique metric on $\{1, 2\}$. Moreover, in this case, there is homogamy (resp. heterogamy) for type-1 if and only if there is homogamy (resp. heterogamy) for type-2. These observations lead to the following definition.

DEFINITION 1.2. *For $k = 2$, the species is said to be homogamous if $\mathbb{P}$-a.s.*

$$\lim_{n \to \infty} \frac{Q_{11}^{(n)}(T_n)}{n} > x_1 y_1,$$

and heterogamous if $\mathbb{P}$-a.s

$$\lim_{n \to \infty} \frac{Q_{11}^{(n)}(T_n)}{n} < x_1 y_1$$

for any infinite population x_1, x_2, y_1, y_2 with $x_1 x_2 y_1 y_2 \neq 0$.

Note that definitions of both panmixia and homogamy/heterogamy assume the existence of the infinite population limit of the normalized mating pattern and that the limit is the same for all sequences of finite populations satisfying (1.2), which are established in Section 2. For the corresponding definitions for finite populations, one has to replace limits with expectations. Also, observe that in the definition of homogamy/heterogamy we exclude the cases where one type is absent, since otherwise the system is trivial and there is panmixia for all choices of parameters.

1.2. **Previous results.** In [8], Gimelfarb introduced two discrete-time models for permanent pair formation: individual and mass encounter-mating. In the first model, at each time step, one single female and one single male are selected, both uniformly at random, to form a temporary pair and this pair becomes permanent exactly as in the Poisson EM model with probability p_{ij}. Observe that if we set, say, $\alpha_i = 0$ and $\beta_j = 1$ for all $i, j \in [k]$, then the dynamics of Gimelfarb's individual encounter-mating model is the same as the embedded discrete-time chain of the pair-type process $Q^{(n)}$ of Poisson EM, and in particular, the mating patterns of the two models coincide. The mass encounter-mating model has a very different encounter mechanism where, at each time step, all the single females and males form temporary pairs according to a permutation chosen uniformly at random, while the mechanism of permanent pair formation from temporary pairs is as before. The main conceptual conclusion of Gimelfarb was that the mating pattern depends not only on the preferences but also on the encounter mechanism. Moreover, given the encounter mechanism, different mating preferences can lead to the same mating pattern. He then stated conditions on the parameters of the models that he conjectured to be sufficient for panmixia, supported the one for mass encounter using a non-rigorous argument, and provided only numerical evidence for the individual encounter case.

In [9], we introduced the stochastic encounter-mating (SEM) model to generalize Gimelfarb's models. The key feature of this generalization is the introduction of firing times which allows one to define a wide range of models and take advantage of their invariance under certain changes of parameters. We investigated in detail the generic case where $p_{ij} = 1$ for all $i, j \in [k]$, that is, there are no preferences, and proved among other things that there is panmixia for all firing time distributions and that the firing times and the mating pattern are independent. As we have already seen, the pair-type process of Poisson EM is a continuous-time Markov process whose rates depend on the parameters of the model through $\pi_{ij} = p_{ij}(\alpha_i + \beta_j)$. Hence, one can play with the parameters without changing the model as long as π_{ij}'s stay the same. Using this and our analysis of the case with no preferences, we concluded that the model exhibits panmixia if it can be changed into a model with no preferences, more precisely, if there are non-negative numbers $\bar{\alpha}_i$ and $\bar{\beta}_j$ such that $\pi_{ij} = p_{ij}(\alpha_i + \beta_j) = 1(\bar{\alpha}_i + \bar{\beta}_j)$ for every $i, j \in [k]$. We record this condition for future reference.

DEFINITION 1.3. *We say that Poisson EM satisfies the fine balance condition if there exist non-negative numbers $\bar{\alpha}_1, \ldots, \bar{\alpha}_k$ and $\bar{\beta}_1, \ldots, \bar{\beta}_k$ such that*

(1.3) $$\pi_{ij} = \bar{\alpha}_i + \bar{\beta}_j, \qquad \forall i, j \in [k].$$

Equivalently,

$$\pi_{ij} + \pi_{i'j'} = \pi_{ij'} + \pi_{i'j}, \quad \forall i, i', j, j' \in [k].$$

The fine balance condition is exactly what Gimelfarb had conjectured in [8] to be sufficient for panmixia. In [9], we not only settled this conjecture, but also used a recursive argument to prove that the fine balance condition is necessary for panmixia. Moreover, under the fine balance condition we gave the distributions of the pair-type process $Q^{(n)}(t)$ and the mating pattern $Q^{(n)}(T_n)$. Finally, we answered the assortative mating question in the case $k = 2$: if $\pi_{11} + \pi_{22} > \pi_{12} + \pi_{21}$, then the (finite) population exhibits homogamy; and if $\pi_{11} + \pi_{22} < \pi_{12} + \pi_{21}$, then it exhibits heterogamy.

1.3. **Overview of results.** In this article, we analyze the Poisson EM model as the population size diverges. In Section 2 we start our investigation by establishing various limit theorems for $Q^{(n)}$. We first prove that the pair-type process rescaled by n converges $\mathbb{P}$-a.s. in the sup norm up to any finite time, where the limiting (deterministic) process $Q(t)$ solves a system of coupled ODEs. More precisely, in Theorem 2.1 we prove that, $\mathbb{P}$-a.s.

$$\lim_{n \to \infty} \sup_{0 \le s \le t} \left| \frac{Q^{(n)}(s)}{n} - Q(s) \right| = 0,$$

where, for every $t > 0$, $Q(t) = (Q_{ij}(t))_{i,j \in [k]}$ satisfies

(1.4) $$\frac{d}{dt} Q_{ij}(t) = \pi_{ij} \frac{\left(x_i - Q_{i,\cdot}(t)\right)\left(y_j - Q_{\cdot,j}(t)\right)}{1 - Q_{tot}(t)}, \quad \text{with} \quad Q_{ij}(0) = 0.$$

This type of generalization of LLN to Markov processes, more precisely, the convergence of a rescaled pure jump Markov process to a (deterministic) solution of a system of ODEs, is known as the fluid limit and is due to [13]. Here, Q represents the infinite population pair-type process and we use the terms pairs, singles etc. for Q as well. As an easy consequence of the fluid limit, we prove that $\mathbb{P}$-a.s. $\lim_{n \to \infty} Q^{(n)}(T_n)/n = Q(\infty)$, that is, the limit as $t \to \infty$ of $Q(t)$ is the mating pattern of the infinite population (see Corollary 2.2). Next, we prove a functional CLT for the process $Q^{(n)}$ and provide an SDE for the weak limit of the rescaled fluctuations (see Theorem 2.3). Finally, we give a diffusion approximation for $Q^{(n)}$ (see Theorem 2.4) which is stronger than the CLT as it is an almost sure limit theorem with concentration bounds. For the proofs of these results we basically follow Chapter 11 of the classical book of Ethier and Kurtz [3].

After establishing these limit theorems we focus on the evolution of Q. In Section 3, we relate the system of ODEs that describe Q to the well-known Lotka-Volterra and replicator equations from population dynamics. Let $X_i(t)$, $Y_j(t)$ and $Z(t)$ denote the number of type-i single females, type-j single males and all single females (or males):

(1.5) $$X_i(t) := x_i - Q_{i,\cdot}(t), \quad Y_j(t) := y_j - Q_{\cdot,j}(t), \quad Z(t) := 1 - Q_{tot}(t).$$

Then, for all $i, j \in [k]$,

(1.6) $$\frac{d}{dt} X_i(t) = -\frac{X_i(t)}{Z(t)} \sum_{j=1}^{k} \pi_{ij} Y_j(t), \quad \frac{d}{dt} Y_j(t) = -\frac{Y_j(t)}{Z(t)} \sum_{i=1}^{k} \pi_{ij} X_i(t),$$

with $X_i(0) = x_i$ and $Y_j(0) = y_j$. Hence, up to a time change due to the $Z(t)$ term, this is a system of $2k$ Lotka-Volterra equations where intrinsic growth (or decay) rate is 0 for all types and sexes. See Theorem 3.1 for the precise statement. Another important equation in population dynamics is the replicator equation, first introduced in [17]. Replicator equations describe the evolution of different

types in a population under density dependent fitness functions and are often used in the context of evolutionary game theory. In general, a Lotka-Volterra equation with l variables is equivalent to a replicator equation with $l+1$ variables, see [10, Theorem 7.5.1]. However, when intrinsic growth rates are constant, one does not need to increase the dimension to obtain a replicator equation. Indeed, the frequencies of types in the Lotka-Volterra system, up to a time change, solve the replicator equation with the same interactions. In particular, we also prove in Theorem 3.1 that, setting $A_i(t) := X_i(t)/Z(t)$ and $B_j(t) := Y_j(t)/Z(t)$ for all $i, j \in [k]$,

(1.7)
$$\frac{d}{dt}A_i(t) = -A_i(t)\left[\sum_{j=1}^{k}\pi_{ij}B_j(t) - \bar{C}(t)\right], \quad \frac{d}{dt}B_j(t) = -B_j(t)\left[\sum_{i=1}^{k}\pi_{ij}A_i(t) - \bar{C}(t)\right],$$

where

$$\bar{C}(t) := \sum_{i=1}^{k}\sum_{j=1}^{k}\pi_{ij}A_i(t)B_j(t).$$

We use (1.5)-(1.7) to deduce that

(1.8)
$$\frac{d}{dt}Z(t) = -Z(t)\sum_{i=1}^{k}\sum_{j=1}^{k}A_i(t)B_j(t).$$

By (1.4), we observe that

(1.9)
$$\frac{d}{dt}Q_{ij}(t) = \pi_{ij}Z(t)A_i(t)B_j(t),$$

and thus find a three-step procedure for obtaining a formula for $Q(t)$: (i) solve the replicator equations (1.7) for A_i's and B_j's; (ii) solve (1.8) to find the total mass $Z(t)$ of the corresponding (time-changed) Lotka-Volterra equations; and finally (iii) solve (1.9).

In Section 3.2, we focus on the fine balance case. We carry out the three-step procedure and obtain a formula for $Q(t)$ for all t, and in particular for the mating pattern $Q(\infty)$. Namely, in Theorem 3.3 we show that

$$A_i(t) = \frac{x_i e^{-\bar{\alpha}_i t}}{\sum_{i'} x_{i'} e^{-\bar{\alpha}_{i'} t}}, \quad B_j(t) = \frac{y_j e^{-\bar{\beta}_j t}}{\sum_{j'} y_{j'} e^{-\bar{\beta}_{j'} t}},$$

$$Q_{ij}(t) = x_i y_j(1 - e^{-\pi_{ij}t}), \quad \text{and} \quad Q_{ij}(\infty) = x_i y_j.$$

Here, recall that $\bar{\alpha}_i$ and $\bar{\beta}_j$ are from the fine balance condition given in Definition 1.3. This verifies the results obtained in [9] for the expectations of the pair-type process and the mating pattern in the finite population setting, albeit this time employing a totally different approach via the replicator equations.

Finally, in Section 4 we study the case $k=2$ with $\pi_{12} = \pi_{21}$ and $x_1 = y_1$. Due to these symmetries, the evolution of the system can be reduced to that of only, say, females. As a result, the corresponding replicator dynamics is one dimensional. More precisely, $A_i(t) = B_i(t)$ for all $t \geq 0$ and $i = 1, 2$, and setting $A_2(t) = 1 - A_1(t)$, we get

(1.10)
$$\frac{d}{dt}A_1(t) = -(\pi_{11} + \pi_{22} - 2\pi_{12})A_1(t)\big(1 - A_1(t)\big)\big(A_1(t) - \gamma\big),$$

where

(1.11)
$$\gamma = \frac{\pi_{22} - \pi_{12}}{\pi_{11} + \pi_{22} - 2\pi_{12}}.$$

Note that in Section 3 we explicitly solve the fine balance case which corresponds to $\pi_{11} + \pi_{22} - 2\pi_{12} = 0$, so we can exclude it, and (1.11) is then well-defined. We give formulas for $Q_{12}(t)$ in terms

of $A_1(t)$ that depend on the value of γ: For $\gamma = 1$

$$Q_{12}(t) = \frac{\theta_1}{1 - x_1} \int_{x_1}^{A_1(t)} \left(\frac{1 - x}{1 - x_1} \right)^{\theta_1 - 1} \left(\frac{x}{x_1} \right)^{-\theta_1 - 1} \exp \left\{ -\theta_1 \left(\frac{1}{1 - x} - \frac{1}{1 - x_1} \right) \right\} dx,$$

for $\gamma = 0$

$$Q_{12}(t) = \frac{\theta_2}{x_1} \int_{1 - x_1}^{1 - A_1(t)} \left(\frac{1 - x}{x_1} \right)^{\theta_2 - 1} \left(\frac{x}{1 - x_1} \right)^{-\theta_2 - 1} \exp \left\{ -\theta_2 \left(\frac{1}{1 - x} - \frac{1}{x_1} \right) \right\} dx,$$

and for $\gamma \notin \{0, 1\}$

$$Q_{12}(t) = -\frac{\pi_{12}(x_1 - \gamma)^{-1}}{\pi_{11} + \pi_{22} - 2\pi_{12}} \int_{x_1}^{A_1(t)} \left(\frac{x}{x_1} \right)^{-\theta_1 - 1} \left(\frac{1 - x}{1 - x_1} \right)^{-\theta_2 - 1} \left(\frac{x - \gamma}{x_1 - \gamma} \right)^{\theta_1 + \theta_2} dx.$$

Here, $\theta_1 = \pi_{12}/(\pi_{22} - \pi_{12})$ and $\theta_2 = \pi_{12}/(\pi_{11} - \pi_{12})$. The stability analysis of A_1 is then carried out simply using (1.10), and we get explicit formulas for the mating pattern. Lastly, we directly use these formulas to give a complete characterization of heterogamy/panmixia/homogamy (see Theorem 4.1), verifying the corresponding result in [9], but this time in the infinite population setting.

1.4. **Discussion and open problems.** Several authors have studied mating models that are similar to the ones in [8], for general references regarding pair formation models see [9]. One article of particular interest is [16], where the ODE describing $Q(t)$ was given for two types and studied numerically.

Panmixia is an important concept in population genetics. It is one of the main assumptions of the Hardy-Weinberg law which states that genotype frequencies remain constant in a population to which no evolutionary force acts on, see e.g. [5]. In the literature, panmixia is also referred to as "random mating", however, this term is obviously misleading since the matings can be random yet assortative. Moreover, this confusion is even greater for a bottom-up approach such as in SEM, where "random mating" suggests that there are no preferences. However, we show in Theorem 3.3 that there are instances where the mating pattern exhibits zero correlations between female and male types even though there are non-trivial preferences.

In the case of assortative mating, the genotype frequencies might differ greatly from the ones predicted by the Hardy-Weinberg law, see [6, Chapter 4] and the references therein. Moreover, assortative mating is one of the key concepts of sexual selection, that is, the evolutionary force driven by mating. In the sexual selection literature, most models of pair formation assume that the females unilaterally accept or reject the males. Various consequences of female choice have been studied in, e.g., [11, 14]. Observe that in the SEM model there is no specification of which sex makes the choice. Actually, this is an advantage of the model: unilateral decisions and choosiness can be incorporated into SEM by appropriately tuning the parameters, while retaining certain degrees of freedom that can be exploited for the purpose of finding exact formulas. However, to enable a self-contained study of sexual selection through SEM we need to extend the model which we discuss next.

SEM is about permanent pair formation and can be seen as a model of monogamous mating of animals in one mating season. Then, one natural direction in which to extend this model is to change the permanent pair structure. A simple way to do this would be to let the pairs separate with a certain rate and send the individuals that form it back to the singles pool. The life-time of a pair corresponds to "latency" in the biological context. These kinds of models are important in the study of the evolution of female choice (via certain payoff functions for staying together with males depending on their types, see, e.g., [4]) and also suitable for studying sexually transmitted diseases, see [2]. SEM can be generalized also by introducing polygamy with each male having a limited number of mates, see [15] for such a model in a simpler setting. Finally, adding offspring production might lead to more general Lotka-Volterra systems.

In Section 2, we use the fluid limit of the pair-type process for large times to prove the LLN for the mating pattern. One can similarly try to establish a CLT for the mating pattern via the functional CLT for the pair-type process. Here, one would need to control the covariance of the fluctuations of the pair-type process as $t \to \infty$. We plan to address this issue in a future work.

In Section 4, we solve the dynamics of the pair-type process in the symmetric 2×2 case, where the corresponding replicator equation is one dimensional. Following a similar strategy, one can try to extend our results to $k = 3$ and get exact formulas for the mating pattern. Phase portraits of all possible Lotka-Volterra equations on the plane, hence, equivalently, of all three dimensional replicator equations, are given in [1]. This suggests that it should be possible to solve the mating pattern problem. However, much less is known for Lotka-Volterra equations in higher dimensions. In particular, numerical simulations show that the behavior in higher dimensions is chaotic and the type of chaos they exhibit is not understood at all, see [7] for an example of chaos with three types.

2. LIMIT THEOREMS

2.1. **The LLN and the fluid limit.** We begin this section by putting Poisson EM into the framework of density dependent families of Markov processes as described in [3, Chapter 11]. For notational convenience we assume WLOG that $x_i^{(n)}/n \le x_i$ and $y_j^{(n)} \le y_j$ for all $i, j \in [k]$ and $n \in \mathbb{N}$. Let

$$(2.1) \qquad \mathcal{E} := \left\{ M \in \mathcal{M}^{k \times k}([0, \infty)) : \ M_{i,\cdot} \le x_i, M_{\cdot,j} \le y_j, \forall i, j \in [k] \right\}.$$

Hence, the state space of the rescaled pair-type process, $n^{-1}Q^{(n)}(t)$, is $\mathcal{E} \cap \mathcal{M}^{k \times k}(n^{-1}\mathbb{N} \cup \{0\})$. Define $F = (F_{ij})_{i,j \in [k]} : \mathcal{E} \to \mathcal{M}^{k \times k}([0, \infty))$ by

$$(2.2) \qquad F_{ij}(M) := \left\{ \begin{array}{ll} \pi_{ij} \frac{\left(x_i - M_{i,\cdot}\right)\left(y_j - M_{\cdot,j}\right)}{1 - M_{tot}} & \text{if } M_{tot} \ne 1, \\ 0 & \text{if } M_{tot} = 1. \end{array} \right.$$

Then, we can rewrite the transition rates of $Q^{(n)}$, given in (1.1), as

$$\rho(M, M + I^{ij}) = nF_{ij}(M/n).$$

Therefore, the processes $\left(n^{-1}Q^{(n)}(t) : t \ge 0\right)$, on state spaces $\mathcal{E} \cap \mathcal{M}^{k \times k}(n^{-1}\mathbb{N} \cup \{0\})$, constitute a density dependent family corresponding to F, as defined in [3, Chapter 11]. Consequently, we have the following representation

$$(2.3) \qquad Q_{ij}^{(n)}(t) = J_{ij}\left(n \int_0^t F_{ij}(n^{-1}Q_{ij}^{(n)}(s))ds\right).$$

Here, $\left\{J_{ij} : \ i, j \in [k]\right\}$ is a collection of independent standard Poisson processes defined on a common probability space $(\Omega, \mathcal{F}, \mathbb{P})$. Therefore, $n^{-1}Q^{(n)}$ is defined for all $n \in \mathbb{N}$ on the same probability space, too.

The following theorem establishes the fluid limit of the rescaled pair-type process, where the limiting process is identified through a coupled system of ODEs.

THEOREM 2.1. *There exists a function $Q = (Q_{ij})_{i,j \in [k]} : [0, \infty) \to \mathcal{E}$ satisfying*

$$(2.4) \qquad Q(t) = \int_0^t F(Q(s))ds,$$

and for any $t \ge 0$, $\mathbb{P}$-a.s.

$$(2.5) \qquad \lim_{n \to \infty} \sup_{0 \le s \le t} \left| \frac{Q^{(n)}(s)}{n} - Q(s) \right| = 0.$$

Proof. First, note that for any $M \in \mathcal{E}$

(2.6)
$$F_{ij}(M) \leq \pi_{ij}(x_i \wedge y_j).$$

Second, we have

(2.7) $\dfrac{\partial F_{ij}(M)}{\partial M_{i'j'}} = \pi_{ij}\left[\left(\dfrac{x_i - M_{i,\cdot}}{1 - M_{tot}}\right)\left(\dfrac{y_j - M_{\cdot,j}}{1 - M_{tot}}\right) - \left(\dfrac{x_i - M_{i,\cdot}}{1 - M_{tot}}\right)\delta_{jj'} - \left(\dfrac{y_j - M_{\cdot,j}}{1 - M_{tot}}\right)\delta_{ii'}\right]$

for every $M \in \mathcal{E}$, where δ_{ij} denotes the Kronecker delta function. This yields

$$\left|\frac{\partial F_{ij}(M)}{\partial M_{i'j'}}\right| \leq \pi_{ij}.$$

Therefore, F is Lipschitz on $\mathcal{E}$ and (2.4) has a unique solution Q. Now we prove that this solution exists for all times. Recall that $\pi_{ij} > 0$ for all $i, j \in [k]$. Thus, $c_1 := \min_{i,j\in[k]} \pi_{ij} > 0$. Setting $c_2 := \max_{i,j\in[k]} \pi_{ij}$ and using (2.2), we get

$$c_1(1 - Q_{tot}(t)) \leq \frac{d}{dt}Q_{tot}(t) \leq c_2(1 - Q_{tot}(t)).$$

Since $Q_{tot}(0) = 0$, this implies

(2.8)
$$1 - e^{-c_1 t} \leq Q_{tot}(t) \leq 1 - e^{-c_2 t}.$$

Thus, $Q_{tot}(t) < 1$ for any t, and as a result, Q exists for all times.

To prove (2.5) we simply need to check that the conditions of [3, Chapter 11, Theorem 2.1] are satisfied. However, these two conditions are boundedness and Lipschitz continuity of F on $\mathcal{E}$, and we have proved them in the previous paragraph. $\qquad\square$

Next, we extend the LLN for the pair-type process to a LLN for the mating pattern. We first describe the state space of $Q^{(n)}(T_n)/n$. Define

$$\mathcal{E}' := \left\{M \in \mathcal{M}^{k\times k}([0,\infty)): \ M_{i,\cdot} = x_i, M_{\cdot,j} = y_j, \forall i,j \in [k]\right\}.$$

As mentioned earlier, at time T_n there are no singles left and thus, $Q^{(n)}(T_n)/n \in \mathcal{E}' \subset \mathcal{E}$. Also note that, for $M \in \mathcal{E}$, $F(M) = 0$ if and only if $M \in \mathcal{E}'$, as a result, using (2.8), we can conclude that $\lim_{t\to\infty} Q(t) =: Q(\infty)$ exists and $Q(\infty) \in \mathcal{E}'$.

COROLLARY 2.2. $\mathbb{P}$-*a.s.*

$$\lim_{n\to\infty} \frac{Q^{(n)}(T_n)}{n} = Q(\infty).$$

Proof. We define

$$T^\delta := \inf\left\{t \geq 0: \ Q_{tot}(t) \geq 1 - \delta\right\}, \quad \delta > 0.$$

By (2.8), we have $T^\delta < \infty$, and $T^\delta \to \infty$ as $\delta \to 0$. Also, it is clear that

(2.9)
$$\left|Q(T^\delta) - Q(\infty)\right| \leq \delta.$$

Now we define the corresponding stopping time for the Markov process $Q^{(n)}$ by

$$T_n^\delta := \inf\{t \geq 0: \ Q_{tot}^{(n)}(t)/n \geq 1 - \delta\}, \quad \delta > 0.$$

Then, since obviously $T_n \geq T_n^\delta$, for any $\delta > 0$ and $n \geq 1$ we have

(2.10)
$$\left|\frac{Q^{(n)}(T_n)}{n} - \frac{Q^{(n)}(T_n^\delta)}{n}\right| \leq \delta.$$

Fix $\delta > 0$. For any $\epsilon < \delta$ we have again $T^{\delta-\epsilon} < \infty$. Thus, via Theorem 2.1, $\mathbb{P}$-a.s., for all n large enough

$$\frac{Q_{tot}^{(n)}(T^{\delta-\epsilon})}{n} \geq Q_{tot}(T^{\delta-\epsilon}) - \epsilon/2 = 1 - \delta + \epsilon/2 > 1 - \delta.$$

Hence, $\mathbb{P}$-a.s., $\limsup_{n\to\infty} T_n^\delta \leq T^{\delta-\epsilon}$. Now we use Theorem 2.1 on the time interval $[0, T^\delta]$. $\mathbb{P}$-a.s., for all n large enough, and for $t \leq T^\delta$ with $Q_{tot}^{(n)}(t)/n \geq 1-\delta$,

$$Q_{tot}(t) \geq \frac{Q_{tot}^{(n)}(t)}{n} - \epsilon/2 \geq 1 - \delta - \epsilon/2 > 1 - \delta - \epsilon.$$

Thus, $t \geq T^{\delta+\epsilon}$ for any such t. Also, for any $t > T^\delta$, since $T^\delta \geq T^{\delta+\epsilon}$, we have $t > T^{\delta+\epsilon}$. Hence, $\mathbb{P}$-a.s., for all n large enough, and $t \geq 0$ with $Q_{tot}^{(n)}(t)/n \geq 1-\delta$, we have $t \geq T^{\delta+\epsilon}$, that is, $\liminf_{n\to\infty} T_n^\delta \geq T^{\delta+\epsilon}$. Since Q_{tot} is continuous, as $\epsilon \to 0$, both $T^{\delta+\epsilon} \to T^\delta$ and $T^{\delta-\epsilon} \to T^\delta$. Therefore, $\mathbb{P}$-a.s., $T_n^\delta \to T^\delta$ as $n \to \infty$. As a result, for any $\epsilon' > 0$ given, $\mathbb{P}$-a.s., for all n large enough $T^\delta - \epsilon' \leq T_n^\delta \leq T^\delta + \epsilon'$. Since $Q_{ij}^{(n)}(t)$ is non-decreasing in t for any $i, j \in [k]$, we have

$$\frac{Q_{ij}^{(n)}(T^\delta - \epsilon')}{n} - Q_{ij}(T^\delta) \leq \frac{Q_{ij}^{(n)}(T_n^\delta)}{n} - Q_{ij}(T^\delta) \leq \frac{Q_{ij}^{(n)}(T^\delta + \epsilon')}{n} - Q_{ij}(T^\delta).$$

Via the inequalities

$$\left| \frac{Q_{ij}^{(n)}(T^\delta - \epsilon')}{n} - Q_{ij}(T^\delta) \right| \leq \left| \frac{Q_{ij}^{(n)}(T^\delta - \epsilon')}{n} - Q_{ij}(T^\delta - \epsilon') \right| + \left| Q_{ij}(T^\delta - \epsilon') - Q_{ij}(T^\delta) \right|$$

and

$$\left| \frac{Q_{ij}^{(n)}(T^\delta + \epsilon')}{n} - Q_{ij}(T^\delta) \right| \leq \left| \frac{Q_{ij}^{(n)}(T^\delta + \epsilon')}{n} - Q_{ij}(T^\delta + \epsilon') \right| + \left| Q_{ij}(T^\delta + \epsilon') - Q_{ij}(T^\delta) \right|,$$

using once again Theorem 2.1, and the fact that Q is continuous, we conclude that $\mathbb{P}$-a.s., as $n \to \infty$

$$(2.11) \qquad \frac{Q^{(n)}(T_n^\delta)}{n} \to Q(T^\delta).$$

Using the triangle inequality, we get

$$\left| \frac{Q^{(n)}(T_n)}{n} - Q(\infty) \right| \leq \left| \frac{Q^{(n)}(T_n)}{n} - \frac{Q^{(n)}(T_n^\delta)}{n} \right| + \left| \frac{Q^{(n)}(T_n^\delta)}{n} - Q(T^\delta) \right| + \left| Q(T^\delta) - Q(\infty) \right|.$$

Finally, (2.9), (2.10) and (2.11) finish the proof. $\qquad\square$

2.2. **The CLT and the diffusion approximation.** In this section, we further assume that the convergence in (1.2) is such that, as $n \to \infty$,

$$\frac{x_i^{(n)} - nx_i}{\sqrt{n}} \to 0 \quad \text{and} \quad \frac{y_j^{(n)} - ny_j}{\sqrt{n}} \to 0.$$

First, we prove the following functional CLT for the pair-type process.

THEOREM 2.3. *Denote by* $V(t) = (V_{ij}(t))$ *the* $\mathcal{M}^{k\times k}(\mathbb{R})$ *valued process satisfying*

$$V_{ij}(t) = W_{ij}\big(Q_{ij}(t)\big) + \sum_{i',j'\in[k]} \int_0^t \frac{\partial F_{ij}(Q(s))}{\partial M_{i'j'}} V_{i'j'}(s)ds,$$

where (W_{ij}) *are independent standard Brownian motions. Then*

$$\frac{Q^{(n)}(\cdot) - nQ(\cdot)}{\sqrt{n}} \Rightarrow V(\cdot)$$

weakly on $D([0,\infty), \mathbb{R})$ *equipped with the topology of uniform convergence on bounded subintervals of* $[0, \infty)$.

Proof. We need to verify the conditions of [3, Chapter 11, Theorem 2.3]. Since $Q(t) \notin \mathcal{E}'$ for any $t \geq 0$, an inspection of the proof of the aforementioned theorem reveals that it is enough to check everything for compact $K \subseteq \mathcal{E} \setminus \mathcal{E}'$. The inequality in (2.23) of [3, Chapter 11, Theorem 2.3] follows immediately from (2.6). The continuity of F_{ij} is obvious. Finally, the continuity of the first partial derivatives of F_{ij} follows from (2.7). This yields weak convergence on $D([0, \infty), \mathbb{R})$ equipped with the Skorohod J_1 topology. However, since V has a.s. continuous paths, weak convergence is valid under the stronger topology of uniform convergence on bounded subintervals of $[0, \infty)$ by [3, Chapter 3, Theorem 10.2]. $\qquad\square$

Next, we give a diffusion approximation for $Q^{(n)}$. Theorem 2.3 describes the fluctuations of $n^{-1}Q^{(n)}$ in distribution. Alternatively, one can find a diffusion process $Z^{(n)}$ defined on the probability space $(\Omega, \mathcal{F}, \mathbb{P})$ and obtain a direct comparison between the two processes. Naturally, the generator of the diffusion process $Z^{(n)}$ approximates that of $n^{-1}Q^{(n)}$ up to the second order term in the Taylor expansion. That is, the generator of $Z^{(n)}$, denoted by $\mathcal{L}^{(n)}$, is given by

$$\mathcal{L}^{(n)}g(M) = \frac{1}{2n} \sum_{i,j \in [k]} F_{ij}(M) \frac{\partial^2 g(M)}{\partial M_{ij}^2} + \sum_{i,j \in [k]} F_{ij}(M) \frac{\partial g(M)}{\partial M_{ij}}.$$

The coupling of $Q^{(n)}/n$ and $Z^{(n)}$ under $\mathbb{P}$ is due to [12] and is also explained in [3, Chapter 7, Corollary 5.5]. Since F_{ij} is continuous on $\mathcal{E}$ for all $i, j \in [k]$, $Z^{(n)}$ can be obtained as the unique solution of

$$Z_{ij}^{(n)}(t) = \frac{1}{n} W_{ij}\left(n \int_0^t F_{ij}(Z^{(n)}(s))ds\right) + \int_0^t F_{ij}(Z^{(n)}(s))ds, \quad i, j \in [k],$$

where W_{ij} are independent standard Brownian motions and are, this time, coupled with J_{ij}'s. See [3, Chapters 7 and 11] for the details of this coupling.

THEOREM 2.4. *Let $T > 0$ be fixed. For $n \geq 2$ there is a random variable Γ_n^T defined on $(\Omega, \mathcal{F}, \mathbb{P})$ and positive constants λ_T, C_T and K_T depending only on T, Π and $x_1, \ldots, x_k, y_1, \ldots, y_k$ such that $\mathbb{P}$-a.s.*

$$\sup_{t \leq T} \left| \frac{Q^{(n)}(t)}{n} - Z^{(n)}(t) \right| \leq \Gamma_n^T \frac{\log n}{n}$$

and

$$\mathbb{P}(\Gamma_n^T > C_T + x) \leq \frac{K_T}{n^2} \exp\left(-\lambda_T \sqrt{x} - \frac{\lambda_T x}{\log n}\right).$$

Proof. Since F_{ij} is Lipschitz on all of $\mathcal{E}$ for every $i, j \in [k]$, we can use [3, Chapter 11, Theorem 3.1], without needing to truncate the time T_n, to conclude the proof. Here, the constants λ_T, C_T and K_T depend only on Π and the type frequencies $x_1, \ldots, x_k, y_1, \ldots, y_k$, because the function F is determined by these parameters. $\qquad\square$

3. ANALYSIS OF THE FLUID LIMIT

3.1. **Lotka-Volterra and replicator equations.** Recall from Section 1 that

$$X_i(t) = x_i - Q_{i,\cdot}(t), \quad Y_j(t) = y_j - Q_{\cdot,j}, \quad Z(t) = 1 - Q_{tot}(t)$$

denote the number of type-i single females, type-j single males, and all single females (or males), respectively. We have also introduced

$$A_i(t) = \frac{X_i(t)}{Z(t)} \quad \text{and} \quad B_j(t) = \frac{Y_j(t)}{Z(t)}.$$

In words, A_i is the fraction of type-i females among all single females, and B_j is the fraction of type-j males among all single males. Then, for any $t \geq 0$,

$$A_1(t) + \cdots + A_k(t) = B_1(t) + \cdots + B_k(t) = 1.$$

For the following we define the $2k \times 2k$ matrix

$$\hat{\Pi} := \begin{pmatrix} 0 & \Pi \\ \Pi^T & 0 \end{pmatrix}.$$

THEOREM 3.1. *Set* $U(t) := \big(X_1(t), \ldots, X_k(t), Y_1(t), \ldots, Y_k(t)\big)$. *Then* U *satisfies*

(3.1) $$\frac{d}{dt}U_i(t) = -\frac{1}{Z(t)}U_i(t)(\hat{\Pi}U(t))_i, \quad i = 1, \ldots, 2k,$$

that is, up to a time change, U *is the solution of a system of Lotka-Volterra equations. Moreover, setting* $C(t) := \frac{1}{2}\big(A_1(t), \ldots, A_k(t), B_1(t), \ldots, B_k(t)\big)$, C *satisfies the following system of replicator equations:*

(3.2) $$\frac{d}{dt}C_i(t) = -2C_i(t)\big((\hat{\Pi}C(t))_i - C^T(t)\hat{\Pi}C(t)\big), \quad i = 1, \ldots, 2k.$$

REMARK 3.2. *When the matrix* Π *is symmetric, which means that its entries do not depend on the sexes but only on the types, and if* $x_i = y_i$ *for all* $i \in [k]$ *it is clear that* $X_i(t) = Y_i(t)$ *and* $A_i(t) = B_i(t)$, *for all* $t \geq 0$ *and* $i \in [k]$. *Consequently, the* $2k$ *replicator equations in (3.2) simplify to the following replicator system with* k *variables:*

(3.3) $$\frac{d}{dt}A_i(t) = -A(t)\big((\Pi A(t))_i - A^T(t)\Pi A(t)\big), \quad i = 1, \ldots, k.$$

We use this observation in Section 4 while studying the symmetric 2×2 *case. A similar simplification also applies to the Lotka-Volterra equations in (3.1).*

Proof of Theorem 3.1. Let us write $X = (X_1, \ldots, X_k)$ and $Y = (Y_1, \ldots, Y_k)$. Using (2.2), (2.4), and the definitions of X_i, Y_j and Z, we get

(3.4) $$\frac{d}{dt}Q_{ij}(t) = \pi_{ij}\frac{X_i(t)Y_j(t)}{Z(t)}.$$

Thus, for $i \in [k]$

(3.5)
$$\frac{d}{dt}U_i(t) = \frac{d}{dt}X_i(t) = -\sum_{j=1}^{k}\frac{d}{dt}Q_{ij}(t) = -\frac{1}{Z(t)}X_i(t)\sum_{j=1}^{k}\pi_{ij}Y_j(t) = -\frac{1}{Z(t)}U_i(t)(\Pi Y(t))_i.$$

Similarly, for $j \in [k]$

(3.6) $$\frac{d}{dt}U_{k+j}(t) = \frac{d}{dt}Y_j(t) = -\frac{1}{Z(t)}U_{k+j}(t)(\Pi^T X(t))_j.$$

Hence, noting that $(\hat{\Pi}U)_i = (\Pi Y)_i$ and $(\hat{\Pi}U)_{k+j} = (\Pi^T X)_j$ for $i, j \in [k]$ gives (3.1). Now summing (3.5) over i (or equivalently (3.6) over j) and using the definitions of A_i and B_j, we get

(3.7) $$\frac{d}{dt}Z(t) = -Z(t)\big(A^T(t)\Pi B(t)\big) = -Z(t)\big(B^T(t)\Pi^T A(t)\big).$$

As a result, using (3.5), for $i \in [k]$

(3.8)
$$2\frac{d}{dt}C_i(t) = \frac{d}{dt}A_i(t) = \frac{d}{dt}X_i(t)\frac{1}{Z(t)} - \frac{X_i(t)}{Z^2(t)}\frac{d}{dt}Z(t)$$
$$= -A_i(t)\big[(\Pi B(t))_i - A^T(t)\Pi B(t)\big].$$

Similarly, using (3.6), for $j \in [k]$

$$(3.9) \qquad 2\frac{d}{dt}C_{k+j}(t) = \frac{d}{dt}B_j(t) = -B_j(t)\left[(\Pi^T A(t))_j - B^T(t)\Pi^T A(t)\right].$$

By the definition of $\hat{\Pi}$ we have

$$(\hat{\Pi}C(t))_i = \frac{1}{2}(\Pi B(t))_i, \quad (\hat{\Pi}C(t))_{k+j} = \frac{1}{2}(\Pi^T A(t))_j, \quad i, j \in [k],$$

and

$$C^T(t)\hat{\Pi}C(t) = \frac{1}{4}A^T(t)\Pi B(t) + \frac{1}{4}B^T(t)\Pi^T A(t) = \frac{1}{2}A^T(t)\Pi B(t) = \frac{1}{2}B^T(t)\Pi^T A(t).$$

Thus, using (3.8), for $i \in [k]$

$$\frac{d}{dt}C_i(t) = \frac{1}{2}\frac{d}{dt}A_i(t) = -2C_i(t)\big((\hat{\Pi}C(t))_i - C^T(t)\hat{\Pi}C(t)\big),$$

and using (3.9), for $j \in [k]$

$$\frac{d}{dt}C_{k+j}(t) = \frac{1}{2}\frac{d}{dt}B_j(t) = -2C_{k+j}(t)\big((\hat{\Pi}C(t))_{k+j} - C^T(t)\hat{\Pi}C(t)\big).$$

Therefore, we are finished with the proof of (3.2). $\qquad\square$

3.2. **Exact solution in the fine balance case.** As we have mentioned in Section 1, in [9] we proved that the fine balance condition, given in Definition 1.3, characterizes panmixia for any finite population. The next theorem gives explicit formulas for the solution of the system of replicator equations and for the pair-type process under the fine balance condition.

THEOREM 3.3. *Assume that the fine balance condition (1.3) is satisfied. Then*

$$A_i(t) = \frac{x_i e^{-\bar{\alpha}_i t}}{\sum_{i'} x_{i'} e^{-\bar{\alpha}_{i'} t}}, \quad B_j(t) = \frac{y_j e^{-\bar{\beta}_j t}}{\sum_{j'} y_{j'} e^{-\bar{\beta}_{j'} t}}$$

and

$$Q_{ij}(t) = x_i y_j(1 - e^{-\pi_{ij} t}).$$

In particular,

$$Q_{ij}(\infty) = x_i y_j.$$

REMARK 3.4. *This result can also be obtained from* [9, Theorem 3.6] *via the fluid limit and the dominated convergence theorem. However, our method here is completely different and self-contained.*

Proof. Using (3.8), for $i \in [k]$ we get

$$(3.10) \qquad \begin{aligned} \frac{d}{dt}\log\big(A_i(t)/A_1(t)\big) &= \frac{d}{dt}\log A_i(t) - \frac{d}{dt}\log A_1(t) \\ &= -\left[(\Pi B(t))_i - A^T(t)\Pi B(t)\right] + \left[(\Pi B(t))_1 - A^T(t)\Pi B(t)\right] \\ &= -\left[(\Pi B(t))_i - (\Pi B(t))_1\right]. \end{aligned}$$

Similarly, by (3.9), for $j \in [k]$ we have

$$(3.11) \qquad \frac{d}{dt}\log\big(B_j(t)/B_1(t)\big) = -\left[(\Pi^T A(t))_j - (\Pi^T A(t))_1\right].$$

Using (1.3), for $i \in [k]$ we get

$$(\Pi B(t))_i = \sum_{j=1}^{k}\pi_{ij}B_j(t) = \sum_{j=1}^{k}(\bar{\alpha}_i + \bar{\beta}_j)B_j(t) = \bar{\alpha}_i + \sum_{j=1}^{k}\bar{\beta}_j B_j(t).$$

Then, (3.10) yields

$$\frac{d}{dt} \log \left(A_i(t)/A_1(t) \right) = -(\bar{\alpha}_i - \bar{\alpha}_1).$$

Hence,

$$\frac{A_i(t)}{A_1(t)} = \frac{A_i(0)}{A_1(0)} e^{-(\bar{\alpha}_i - \bar{\alpha}_1)t}.$$

Finally, since $A_1(t) + \cdots + A_k(t) = 1$, we get

$$A_i(t) = \frac{x_i e^{-\bar{\alpha}_i t}}{\bar{A}(t)}, \quad \text{where} \quad \bar{A}(t) = \sum_{i'=1}^{k} x_{i'} e^{-\bar{\alpha}_{i'} t}$$

is the normalization term. Similarly, using (3.11), we get

$$B_j(t) = \frac{y_j e^{-\bar{\beta}_j t}}{\bar{B}(t)}, \quad \text{where} \quad \bar{B}(t) = \sum_{j'=1}^{k} y_{j'} e^{-\bar{\beta}_{j'} t}.$$

Next, we compute $Z(t)$. Note that we can use (3.7) to write

$$
\begin{aligned}
\frac{d}{dt} \log Z(t) = -A^T(t) \Pi B(t) &= -\sum_{i=1}^{k} \sum_{j=1}^{k} (\bar{\alpha}_i + \bar{\beta}_j) A_i(t) B_j(t) \\
&= -\sum_{i=1}^{k} \sum_{j=1}^{k} \bar{\alpha}_i A_i(t) B_j(t) - \sum_{i=1}^{k} \sum_{j=1}^{k} \bar{\beta}_j A_i(t) B_j(t) \\
&= -\sum_{i=1}^{k} \bar{\alpha}_i A_i(t) - \sum_{j=1}^{k} \bar{\beta}_j B_j(t) \\
&= -\sum_{i=1}^{k} \frac{x_i \bar{\alpha}_i e^{-\bar{\alpha}_i t}}{\bar{A}(t)} - \sum_{j=1}^{k} \frac{y_j \bar{\beta}_j e^{-\bar{\beta}_j t}}{\bar{B}(t)} \\
&= \frac{1}{\bar{A}(t)} \frac{d}{dt} \bar{A}(t) + \frac{1}{\bar{B}(t)} \frac{d}{dt} \bar{B}(t) = \frac{d}{dt} \log \bar{A}(t) + \frac{d}{dt} \log \bar{B}(t) = \frac{d}{dt} \log \left[\bar{A}(t) \bar{B}(t) \right].
\end{aligned}
$$

Since $\bar{A}(0) = \bar{B}(0) = Z(0) = 1$, we conclude that

$$Z(t) = \bar{A}(t) \bar{B}(t) = \sum_{i=1}^{k} x_i e^{-\bar{\alpha}_i t} \sum_{j=1}^{k} y_j e^{-\bar{\beta}_j t} = \sum_{i=1}^{k} \sum_{j=1}^{k} x_i y_j e^{-\pi_{ij} t}.$$

Finally, we compute $Q_{ij}(t)$. We can use (3.4) to write

$$\frac{d}{dt} Q_{ij}(t) = \pi_{ij} Z(t) A_i(t) B_j(t) = \pi_{ij} \bar{A}(t) \bar{B}(t) \frac{x_i e^{-\bar{\alpha}_i t}}{\bar{A}(t)} \frac{y_j e^{-\bar{\beta}_j t}}{\bar{B}(t)} = \pi_{ij} x_i y_j e^{-\pi_{ij} t}.$$

Finally, $Q_{ij}(0) = 0$ yields

$$Q_{ij}(t) = x_i y_j \left[1 - e^{-\pi_{ij} t} \right].$$

$\square$

4. The symmetric 2×2 case

In this section we use the shorthand notation $\dot{f}$ to denote the time derivative $\frac{d}{dt}f(t)$ of any function f. We assume that $k = 2$, $\pi_{12} = \pi_{21}$ and $x_1 = y_1$. Setting $A_2 = 1 - A_1$, the replicator equation in (3.3) becomes a one dimensional ODE given by

$$(4.1) \qquad \dot{A}_1 = -A_1(1 - A_1)\Big[(\pi_{11} + \pi_{22} - 2\pi_{12})A_1 - (\pi_{22} - \pi_{12})\Big],$$

with $A_1(0) = x_1$, and (3.7) is equivalent to

$$(4.2) \qquad \frac{\dot{Z}}{Z} = -(\pi_{11} + \pi_{22} - 2\pi_{12})A_1^2 + 2(\pi_{22} - \pi_{12})A_1 - \pi_{22},$$

with $Z(0) = 1$. We already solved for Q in the previous section under the fine balance condition so we exclude that case, i.e., we assume that $\pi_{11} + \pi_{22} \neq 2\pi_{12}$. Hence, setting

$$\gamma = \frac{\pi_{22} - \pi_{12}}{\pi_{11} + \pi_{22} - 2\pi_{12}},$$

the equation in (4.1) becomes

$$(4.3) \qquad \dot{A}_1 = -(\pi_{11} + \pi_{22} - 2\pi_{12})A_1(1 - A_1)(A_1 - \gamma).$$

Recall that our goal is to find a formula for the mating pattern. As we discussed in Section 1, when $k = 2$ it suffices to find $Q_{12}(\infty)$ because

$$Q_{11}(\infty) = x_1 - Q_{12}(\infty), \quad Q_{21}(\infty) = y_1 - Q_{11}(\infty), \quad \text{and} \quad Q_{22}(\infty) = x_2 - Q_{21}(\infty).$$

For this we use (3.4), which can be written in the form

$$(4.4) \qquad \dot{Q}_{12} = \pi_{12}ZA_1(1 - A_1).$$

We first study the case $\gamma \in \{0, 1\}$, that is, $\pi_{11} = \pi_{12}$ or $\pi_{22} = \pi_{12}$.

4.1. $\gamma \in \{0, 1\}$.

We investigate the case $\gamma = 1$, that is, $\pi_{11} = \pi_{12}$, the case $\gamma = 0$ is analogous.

Note that (4.3) and (4.2) become, respectively,

$$(4.5) \qquad \dot{A}_1 = (\pi_{22} - \pi_{12})A_1(1 - A_1)^2$$

and

$$(4.6) \qquad \frac{\dot{Z}}{Z} = -(\pi_{22} - \pi_{12})(1 - A_1)^2 - \pi_{12}.$$

We can use partial fractions to write (4.5) as

$$\left(\frac{1}{A_1} + \frac{1}{1 - A_1} + \frac{1}{(1 - A_1)^2} \right) \dot{A}_1 = \pi_{22} - \pi_{12}.$$

Integrating both sides and using the initial condition $A_1(0) = x_1$, we get

$$(4.7) \qquad \frac{(1 - x_1)A_1(t)}{x_1(1 - A_1(t))} \exp\left\{ \frac{1}{1 - A_1(t)} - \frac{1}{1 - x_1} \right\} = e^{(\pi_{22} - \pi_{12})t}.$$

This is an implicit formula for $A_1(t)$.

Next, we find a formula for $Z(t)$. We know from (4.5) that

$$(\pi_{22} - \pi_{12})(1 - A_1)^2 = \frac{\dot{A}_1}{A_1}.$$

Substituting this in (4.6), we see that

$$\frac{\dot{Z}}{Z} = -\frac{\dot{A}_1}{A_1} - \pi_{12}.$$

Integrating both sides and using the initial condition $Z(0) = 1$, we get

(4.8)
$$Z(t) = \left(\frac{x_1}{A_1(t)} \right) e^{-\pi_{12}t}.$$

We can express $Z(t)$ in terms of $A_1(t)$ only (i.e., without any explicit t dependence.) Indeed, raising both sides of (4.7) to power $-\theta_1$ where

$$\theta_1 := \frac{\pi_{12}}{\pi_{22} - \pi_{12}}$$

gives

$$\left(\frac{(1 - x_1)A_1(t)}{x_1(1 - A_1(t))} \right)^{-\theta_1} \exp \left\{ -\theta_1 \left(\frac{1}{1 - A_1(t)} - \frac{1}{1 - x_1} \right) \right\} = e^{-\pi_{12}t}.$$

Plugging this into the RHS of (4.8), we get

(4.9)
$$Z(t) = \left(\frac{1 - A_1(t)}{1 - x_1} \right)^{\theta_1} \left(\frac{A_1(t)}{x_1} \right)^{-\theta_1 - 1} \exp \left\{ -\theta_1 \left(\frac{1}{1 - A_1(t)} - \frac{1}{1 - x_1} \right) \right\}.$$

Finally, we express $Q_{12}(t)$ in terms of $A_1(t)$. We put (4.5) in the form

$$A_1(1 - A_1) = \frac{\dot{A}_1}{(\pi_{22} - \pi_{12})(1 - A_1)}.$$

We can use this and (4.9) to write

$$\dot{Q}_{12} = \pi_{12}ZA_1(1 - A_1) = \frac{\theta_1 Z \dot{A}_1}{(1 - A_1)}$$

$$= \frac{\theta_1}{1 - x_1} \left(\frac{1 - A_1}{1 - x_1} \right)^{\theta_1 - 1} \left(\frac{A_1}{x_1} \right)^{-\theta_1 - 1} \exp \left\{ -\theta_1 \left(\frac{1}{1 - A_1} - \frac{1}{1 - x_1} \right) \right\} \dot{A}_1.$$

Integrating both sides, using the initial conditions $A_1(0) = x_1$ and $Q_{12}(0) = 0$, and making a change of variables, we get

$$Q_{12}(t) = \frac{\theta_1}{1 - x_1} \int_{x_1}^{A_1(t)} \left(\frac{1 - x}{1 - x_1} \right)^{\theta_1 - 1} \left(\frac{x}{x_1} \right)^{-\theta_1 - 1} \exp \left\{ -\theta_1 \left(\frac{1}{1 - x} - \frac{1}{1 - x_1} \right) \right\} dx$$

$$= x_1 \theta_1 \int_{1}^{\zeta(t)} x^{-(\theta_1 + 1)} e^{-\left(\frac{x_1}{1 - x_1} \right)\theta_1(x - 1)} dx$$

where

$$\zeta(t) = \frac{(1 - x_1)A_1(t)}{x_1(1 - A_1(t))}.$$

If $\pi_{11} = \pi_{12} < \pi_{22}$, then it is easy to see from the stability analysis of (4.5) that

$$\lim_{t \to \infty} A_1(t) = 1 \quad \text{and, hence,} \quad \lim_{t \to \infty} \zeta(t) = \infty.$$

Therefore, the mating pattern has the following formula:

(4.10)
$$Q_{12}(\infty) = x_1 \theta_1 \int_{1}^{\infty} x^{-(\theta_1 + 1)} e^{-\left(\frac{x_1}{1 - x_1} \right)\theta_1(x - 1)} dx = \int_{0}^{\infty} \left(1 + \frac{y}{x_1 \theta_1} \right)^{-\theta_1 - 1} e^{-\frac{y}{1 - x_1}} dy.$$

Here, observe that $\theta_1 > 0$. Similarly, if $\pi_{11} = \pi_{12} > \pi_{22}$, then

$$\lim_{t \to \infty} A_1(t) = 0 \quad \text{and, hence,} \quad \lim_{t \to \infty} \zeta(t) = 0.$$

Therefore, the mating pattern has the following formula:

$$Q_{12}(\infty) = -x_1\theta_1 \int_0^1 x^{-(\theta_1+1)} e^{-\left(\frac{x_1}{1-x_1}\right)\theta_1(x-1)} dx$$

$$= \int_0^{-x_1\theta_1} \left(1 + \frac{y}{x_1\theta_1}\right)^{-\theta_1-1} e^{-\frac{y}{1-x_1}} dy.$$

Here, observe that $\theta_1 < 0$.

For $\gamma = 0$, that is, $\pi_{22} = \pi_{12}$, we relabel type-1 individuals as type-2 and type-2 individuals as type-1 (for each sex). Hence, we have once again the situation where $\gamma = 1$. Also, observe that $Q_{12}(t) = Q_{21}(t)$ for all since $X_i(t) = Y_i(t)$ for all $t \geq 0$. Hence, we get formulas for $Q_{12}(\infty)$ analogous to the ones in (4.10) and (4.11) by simply swapping π_{11} with π_{22} and x_1 with $1 - x_1$ (recall that $x_2 = 1 - x_1$). More precisely, setting

$$\theta_2 = \frac{\pi_{12}}{\pi_{11} - \pi_{12}},$$

we have

$$Q_{12}(t) = \frac{\theta_2}{x_1} \int_{1-x_1}^{1-A_1(t)} \left(\frac{1-x}{x_1}\right)^{\theta_2-1} \left(\frac{x}{1-x_1}\right)^{-\theta_2-1} \exp\left\{-\theta_2\left(\frac{1}{1-x} - \frac{1}{x_1}\right)\right\} dx.$$

As before, by the stability analysis of $A_1(t)$, we have the following formulas for the mating pattern. If $\pi_{22} = \pi_{12} < \pi_{11}$

$$Q_{12}(\infty) = (1 - x_1)\theta_2 \int_1^\infty x^{-(\theta_2+1)} e^{-\left(\frac{1-x_1}{x_1}\right)\theta_2(x-1)} dx$$

$$= \int_0^\infty \left(1 + \frac{y}{(1-x_1)\theta_2}\right)^{-\theta_2-1} e^{-\frac{y}{x_1}} dy,$$

where $\theta_2 > 0$. If $\pi_{22} = \pi_{12} > \pi_{11}$

$$Q_{12}(\infty) = -(1 - x_1)\theta_2 \int_0^1 x^{-(\theta_2+1)} e^{-\left(\frac{1-x_1}{x_1}\right)\theta_2(x-1)} dx$$

$$= \int_0^{-(1-x_1)\theta_2} \left(1 + \frac{y}{(1-x_1)\theta_2}\right)^{-\theta_2-1} e^{-\frac{y}{x_1}} dy,$$

where $\theta_2 < 0$.

4.2. $\gamma \notin \{0, 1\}$. $x_1 = \gamma$ constitutes a special case and we study it first.

4.2.1. $x_1 = \gamma \in (0, 1)$. By (4.3) we have $\dot{A}_1 = 0$ and, therefore, $A_1(t) = x_1$. Plugging this in (4.2) gives

$$\frac{\dot{Z}}{Z} = -\pi_{12}x_1 - \pi_{22}(1 - x_1).$$

Using the initial condition $Z(0) = 1$, we get

$$Z(t) = e^{-(\pi_{12}x_1 + \pi_{22}(1-x_1))t}.$$

Finally,

$$\dot{Q}_{12} = \pi_{12}ZA_1(1 - A_1) = \pi_{12}x_1(1 - x_1)e^{-(\pi_{12}x_1 + \pi_{22}(1-x_1))t}$$

is easily solved with initial condition $Q_{12}(0) = 0$ to get

$$Q_{12}(t) = \frac{\pi_{12}x_1(1 - x_1)}{\pi_{12}x_1 + \pi_{22}(1 - x_1)} \left(1 - e^{-(\pi_{12}x_1 + \pi_{22}(1-x_1))t}\right).$$

In particular, the mating pattern is given by

$$(4.12) \quad Q_{12}(\infty) = \frac{\pi_{12}x_1(1-x_1)}{\pi_{12}x_1 + \pi_{22}(1-x_1)} = x_1(1-x_1)\left[\frac{\pi_{12}(\pi_{11}+\pi_{22}-2\pi_{12})}{\pi_{12}(\pi_{22}-\pi_{12})+\pi_{22}(\pi_{11}-\pi_{12})}\right].$$

Note that, by the definitions of θ_1 and θ_2, we have

$$1 + \frac{1}{\theta_1 + \theta_2} = \frac{\pi_{12}(\pi_{22}-\pi_{12})+\pi_{22}(\pi_{11}-\pi_{12})}{\pi_{12}(\pi_{11}+\pi_{22}-2\pi_{12})}.$$

Hence, we get

$$Q_{12}(\infty) = \frac{x_1(1-x_1)}{1+\frac{1}{\theta_1+\theta_2}}.$$

4.2.2. $x_1 \neq \gamma$. Using partial fractions, (4.3) can be written as

$$(4.13) \quad \left(-\frac{1}{\gamma A_1} + \frac{1}{\gamma(1-\gamma)(A_1-\gamma)} + \frac{1}{(1-\gamma)(1-A_1)}\right)\dot{A}_1 = -(\pi_{11}+\pi_{22}-2\pi_{12}).$$

It is clear from (4.3) that $A_1(t)$ never crosses γ. Integrating both sides of (4.13) and using the initial condition $A_1(0) = x_1$, we get

$$\left(\frac{x_1(A_1(t)-\gamma)}{(x_1-\gamma)A_1(t)}\right)^{\frac{1}{\gamma}}\left(\frac{(1-x_1)(A_1(t)-\gamma)}{(x_1-\gamma)(1-A_1(t))}\right)^{\frac{1}{1-\gamma}} = e^{-(\pi_{11}+\pi_{22}-2\pi_{12})t}.$$

Raising both sides to power $\frac{\pi_{12}}{\pi_{11}+\pi_{22}-2\pi_{12}}$ gives

$$(4.14) \quad \left(\frac{x_1(A_1(t)-\gamma)}{(x_1-\gamma)A_1(t)}\right)^{\theta_1}\left(\frac{(1-x_1)(A_1(t)-\gamma)}{(x_1-\gamma)(1-A_1(t))}\right)^{\theta_2} = e^{-\pi_{12}t}.$$

This is an implicit formula for $A_1(t)$.

Next, we find a formula for $Z(t)$. We can rewrite (4.2) as

$$(4.15) \quad \frac{\dot{Z}}{Z} = -(\pi_{11}+\pi_{22}-2\pi_{12})A_1(A_1-\gamma) - \pi_{12}A_1 - \pi_{22}(1-A_1).$$

Note that (4.3) gives

$$-(\pi_{11}+\pi_{22}-2\pi_{12})A_1(A_1-\gamma) = \frac{\dot{A}_1}{1-A_1},$$

$$-A_1 = \frac{\dot{A}_1}{(\pi_{11}+\pi_{22}-2\pi_{12})(A_1-\gamma)(1-A_1)}, \quad \text{and}$$

$$-(1-A_1) = \frac{\dot{A}_1}{(\pi_{11}+\pi_{22}-2\pi_{12})A_1(A_1-\gamma)}.$$

Substituting these into the RHS of (4.15) and using partial fractions, we get

$$\frac{\dot{Z}}{Z} = \left(\frac{1}{1-A_1} + \frac{\pi_{12}}{(\pi_{11}+\pi_{22}-2\pi_{12})(A_1-\gamma)(1-A_1)} + \frac{\pi_{22}}{(\pi_{11}+\pi_{22}-2\pi_{12})A_1(A_1-\gamma)}\right)\dot{A}_1$$

$$= \left(-\frac{\theta_1+1}{A_1} + \frac{\theta_2+1}{1-A_1} + \frac{\theta_1+\theta_2+1}{A_1-\gamma}\right)\dot{A}_1.$$

We integrate both sides, use the initial conditions $A_1(0) = x_1$ and $Z(0) = 1$, and (4.14) to deduce that

$$\text{(4.16)} \quad Z(t) = \left(\frac{A_1(t)}{x_1}\right)^{-\theta_1-1} \left(\frac{1-A_1(t)}{1-x_1}\right)^{-\theta_2-1} \left(\frac{A_1(t)-\gamma}{x_1-\gamma}\right)^{\theta_1+\theta_2+1}$$

$$= \left(\frac{x_1(1-x_1)(A_1(t)-\gamma)}{(x_1-\gamma)A_1(t)(1-A_1(t))}\right) \left(\frac{x_1(A_1(t)-\gamma)}{(x_1-\gamma)A_1(t)}\right)^{\theta_1} \left(\frac{(1-x_1)(A_1(t)-\gamma)}{(x_1-\gamma)(1-A_1(t))}\right)^{\theta_2}$$

$$\text{(4.17)} \quad = \left(\frac{x_1(1-x_1)(A_1(t)-\gamma)}{(x_1-\gamma)A_1(t)(1-A_1(t))}\right) e^{-\pi_{12}t}.$$

Here, (4.16) is in terms of $A_1(t)$ only. On the other hand, (4.17) is somewhat simpler.

Finally, we provide a formula for the limiting pair-type process. Note that (4.3) gives

$$A_1(1-A_1) = -\frac{\dot{A}_1}{(\pi_{11}+\pi_{22}-2\pi_{12})(A_1-\gamma)}.$$

Using this and (4.16), we get

$$\dot{Q}_{12} = \pi_{12}ZA_1(1-A_1)$$

$$= -\frac{\pi_{12}(x_1-\gamma)^{-1}}{\pi_{11}+\pi_{22}-2\pi_{12}} \left(\frac{A_1}{x_1}\right)^{-\theta_1-1} \left(\frac{1-A_1}{1-x_1}\right)^{-\theta_2-1} \left(\frac{A_1-\gamma}{x_1-\gamma}\right)^{\theta_1+\theta_2} \dot{A}_1.$$

Integrating both sides, using the initial conditions $A_1(0) = x_1$ and $Q_{12}(0) = 0$, and making a change of variables, we get

$$Q_{12}(t) = -\frac{\pi_{12}(x_1-\gamma)^{-1}}{\pi_{11}+\pi_{22}-2\pi_{12}} \int_{x_1}^{A_1(t)} \left(\frac{x}{x_1}\right)^{-\theta_1-1} \left(\frac{1-x}{1-x_1}\right)^{-\theta_2-1} \left(\frac{x-\gamma}{x_1-\gamma}\right)^{\theta_1+\theta_2} dx$$

$$= \frac{\pi_{12}}{\pi_{11}+\pi_{22}-2\pi_{12}} \int_0^{\xi(t)} \left(1+\frac{\gamma y}{x_1}\right)^{-\theta_1-1} \left(1+\frac{(1-\gamma)y}{1-x_1}\right)^{-\theta_2-1} dy$$

where

$$\xi(t) = \frac{x_1-A_1(t)}{A_1(t)-\gamma}.$$

In particular, the mating pattern is given by

$$\text{(4.18)} \quad Q_{12}(\infty) = \frac{\pi_{12}}{\pi_{11}+\pi_{22}-2\pi_{12}} \int_0^{\xi(\infty)} \left(1+\frac{\gamma y}{x_1}\right)^{-\theta_1-1} \left(1+\frac{(1-\gamma)y}{1-x_1}\right)^{-\theta_2-1} dy.$$

The value of $\xi(\infty)$ can be deduced from (4.3) using stability analysis:

(i) If $\pi_{11} > \pi_{12}$ and $\pi_{22} > \pi_{12}$, then $0 < \gamma < 1$, $A_1(\infty) = \gamma$ and $\xi(\infty) = \infty$.

(ii) If $\pi_{11} < \pi_{12}$ and $\pi_{22} < \pi_{12}$, then $0 < \gamma < 1$ and there are two subcases.
- If $x_1 < \gamma$, then $A_1(\infty) = 0$ and $\xi(\infty) = -x_1/\gamma$.
- If $x_1 > \gamma$, then $A_1(\infty) = 1$ and $\xi(\infty) = -(1-x_1)/(1-\gamma)$.

(iii) If $\pi_{11} > \pi_{12}$ and $\pi_{22} < \pi_{12}$, then there are two subcases.
- If $\pi_{11} + \pi_{22} < 2\pi_{12}$, then $\gamma > 1$, $A_1(\infty) = 0$ and $\xi(\infty) = -x_1/\gamma$.
- If $\pi_{11} + \pi_{22} > 2\pi_{12}$, then $\gamma < 0$, $A_1(\infty) = 0$ and $\xi(\infty) = -x_1/\gamma$.

(iv) If $\pi_{11} < \pi_{12}$ and $\pi_{22} > \pi_{12}$, then there are two subcases.
- If $\pi_{11} + \pi_{22} < 2\pi_{12}$, then $\gamma < 0$, $A_1(\infty) = 1$ and $\xi(\infty) = -(1-x_1)/(1-\gamma)$.
- If $\pi_{11} + \pi_{22} > 2\pi_{12}$, then $\gamma > 1$, $A_1(\infty) = 1$ and $\xi(\infty) = -(1-x_1)/(1-\gamma)$.

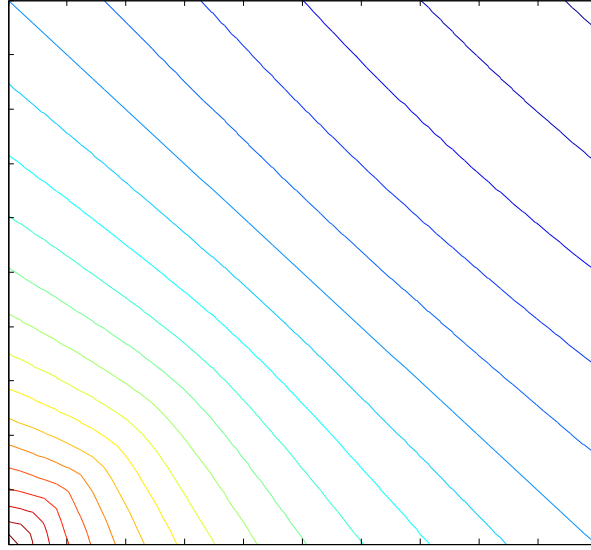Hence, we have an explicit formula for the mating pattern in each case.

FIGURE 1. Level curves of $Q_{12}(\infty)$ as a function of π_{11} (x-axis) and π_{22} (y-axis) for fixed $\pi_{12} = \pi_{21} = 1/2$ and $x_1 = x_2 = y_1 = y_2 = 1/2$. The value of $Q_{12}(\infty)$ on each level curve is separated by 1/64. The diagonal line $\pi_{11} + \pi_{22} = 1$ corresponds to panmixia.

4.3. **Characterization of heterogamy/panmixia/homogamy.** Having established explicit formulas for the mating pattern, we analyze these formulas to prove the following trichotomy result for the assortativeness of Poisson EM.

THEOREM 4.1. *The species is*

  (i) *heterogamous if* $\pi_{11} + \pi_{22} < 2\pi_{12}$,
 (ii) *panmictic if* $\pi_{11} + \pi_{22} = 2\pi_{12}$,
(iii) *homogamous if* $\pi_{11} + \pi_{22} > 2\pi_{12}$.

Proof. We already showed in Theorem 3.3 that $Q_{ij}(\infty) = x_i y_j$ under the fine balance assumption. Hence, part (ii) of Theorem 4.1 has been proven, actually, in a much more general setup.

Part (i) is equivalent to part (iii), simply by relabeling. More precisely, we relabel, say, males, that is, we relabel type-1 males as type-2 males and type-2 males as type-1 males. Then, in this new relabeled model, at all times, the number of type-1 single females is equal to the number of type-2 single males, and the number of type-2 single females is equal to the number of type-1 single males (we have the same initial conditions as before). The equations in (4.3) and (4.2) stay the same, moreover, the type-11 pair-type process of the relabeled model is the same as the type-12 pair-type process of the original model. Thus, we only need to prove (iii), so we assume that $\pi_{11} + \pi_{22} > 2\pi_{12}$. We proceed with the proof by analyzing the formula we have found for $Q_{12}(\infty)$ which depends on γ.

$\gamma \in \{0, 1\}$: Consider the case $\gamma = 1$, that is, $\pi_{11} = \pi_{12}$. Since we assume that $\pi_{11} + \pi_{22} > 2\pi_{12}$ we have $\pi_{11} = \pi_{12} < \pi_{22}$. Then (4.10) holds for the mating pattern:

$$Q_{12}(\infty) = \int_0^\infty \left(1 + \frac{y}{x_1 \theta_1}\right)^{-\theta_1 - 1} e^{-\frac{y}{1 - x_1}} \, dy,$$

with $\theta_1 > 0$. Note that, since $e^y > (1 + y/c)^c$ for any $c, y > 0$, we have

$$e^{-\frac{y}{1 - x_1}} < \left(1 + \frac{y}{x_1 \theta_1}\right)^{-\frac{x_1}{1 - x_1} \theta_1}$$

for every $y > 0$. Therefore,

$$Q_{12}(\infty) < \int_0^\infty \left(1 + \frac{y}{x_1\theta_1} \right)^{-\theta_1 - 1 - \frac{x_1}{1-x_1}\theta_1} dy = x_1(1-x_1),$$

i.e., we have homogamy. The proof of homogamy for $\gamma = 0$, that is, $\pi_{22} = \pi_{12}$, is exactly the same.

$\underline{\gamma \notin \{0,1\}}$: In the case where $x_1 = \gamma \in (0,1)$, recall that

$$Q_{12}(\infty) = \frac{x_1(1-x_1)}{1 + \frac{1}{\theta_1 + \theta_2}}.$$

Since $\gamma \in (0,1)$ and $\pi_{11} + \pi_{22} > 2\pi_{12}$, we have $\pi_{11} > \pi_{12}$ and $\pi_{22} > \pi_{12}$. Hence, $\theta_1 + \theta_2 > 0$, which implies that $Q_{12}(\infty) < x_1(1-x_1)$, and we have homogamy.

Now assume that $x_1 \neq \gamma$. We consider first the case $\pi_{11} > \pi_{12}$ and $\pi_{22} > \pi_{12}$. Then $\gamma \in (0,1)$, $A_1(\infty) = \gamma$, $\xi(\infty) = \infty$, and $\theta_1, \theta_2 > 0$. By the formula in (4.18) we have

$$Q_{12}(\infty) = \theta_1\gamma \int_0^\infty \left(1 + \frac{\gamma y}{x_1} \right)^{-(\theta_1+1)} \left(1 + \frac{(1-\gamma)y}{1-x_1} \right)^{-(\theta_2+1)} dy.$$

If $x_1 > \gamma$, then

(4.19)
$$0 < \frac{1-x_1}{1-\gamma} < 1 < \frac{x_1}{\gamma}.$$

Thus, since $(1 + y/c_1)^{c_1} < (1 + y/c_2)^{c_2}$ for every $y > 0$ and $0 < c_1 < c_2$, we get

$$\left(1 + \frac{(1-\gamma)y}{1-x_1} \right)^{\frac{1-x_1}{1-\gamma}} < \left(1 + \frac{\gamma y}{x_1} \right)^{\frac{x_1}{\gamma}}$$

for every $y > 0$. The above inequality gives

$$\left(1 + \frac{\gamma y}{x_1} \right)^{-(\theta_1+1)} < \left(1 + \frac{(1-\gamma)y}{1-x_1} \right)^{-(\theta_1+1)\frac{\gamma(1-x_1)}{(1-\gamma)x_1}}.$$

Therefore,

$$Q_{12}(\infty) < \theta_1\gamma \int_0^\infty \left(1 + \frac{(1-\gamma)y}{1-x_1} \right)^{-(\theta_1+1)\frac{\gamma(1-x_1)}{(1-\gamma)x_1} - (\theta_2+1)} dy = \frac{x_1(1-x_1)}{1 + (1-x_1)/\theta_1} < x_1(1-x_1),$$

and we have homogamy. Similarly, if $x_1 < \gamma$, then we get

$$Q_{12}(\infty) < \frac{x_1(1-x_1)}{1 + x_1/\theta_2} < x_1(1-x_1).$$

In particular, we again have homogamy.

Next, consider the case $\pi_{11} > \pi_{12} > \pi_{22}$. Then $\gamma < 0$, $A_1(\infty) = 0$, $\xi(\infty) = -x_1/\gamma$, $\theta_2 > 0$, $\theta_1 < -1$ and $\theta_1 + \theta_2 < 0$. By (4.18), we have

$$Q_{12}(\infty) = \theta_1\gamma \int_0^{-x_1/\gamma} \left(1 + \frac{\gamma y}{x_1} \right)^{-(\theta_1+1)} \left(1 + \frac{(1-\gamma)y}{1-x_1} \right)^{-(\theta_2+1)} dy.$$

Since $\gamma < 0$,

(4.20)
$$\frac{1-x_1}{1-\gamma} > 0 > \frac{x_1}{\gamma},$$

which implies

(4.21)
$$\left(1 + \frac{\gamma y}{x_1} \right)^{\frac{x_1}{\gamma}} > \left(1 + \frac{(1-\gamma)y}{1-x_1} \right)^{\frac{1-x_1}{1-\gamma}}$$

for every $y \in (0, -x_1/\gamma)$. Note that $(1 - \gamma)\theta_2 = \gamma\theta_1$. Hence, raising both sides of the above inequality to power $-\frac{\gamma\theta_1}{\gamma - x_1} = -\frac{(1-\gamma)\theta_2}{\gamma - x_1} > 0$, we get

$$\left(1 + \frac{\gamma y}{x_1}\right)^{-\frac{x_1\theta_1}{\gamma - x_1}} > \left(1 + \frac{(1-\gamma)y}{1 - x_1}\right)^{-\frac{(1-x_1)\theta_2}{\gamma - x_1}}.$$

Therefore,

$$Q_{12}(\infty) < \theta_1\gamma \int_0^{-x_1/\gamma} \left(1 + \frac{\gamma y}{x_1}\right)^{-(\theta_1+1)-\frac{x_1\theta_1}{\gamma - x_1}} \left(1 + \frac{(1-\gamma)y}{1 - x_1}\right)^{-(\theta_2+1)+\frac{(1-x_1)\theta_2}{\gamma - x_1}} dy$$

$$= \theta_1\gamma \int_0^{-x_1/\gamma} \left(\frac{1 + \frac{\gamma y}{x_1}}{1 + \frac{(1-\gamma)y}{1-x_1}}\right)^{-\frac{\theta_1\gamma}{\gamma - x_1}-1} \left(1 + \frac{(1-\gamma)y}{1 - x_1}\right)^{-2} dy$$

$$= x_1(1 - x_1) \left(\frac{\theta_1\gamma}{x_1 - \gamma}\right) \int_0^1 u^{-\frac{\theta_1\gamma}{\gamma - x_1}-1} du$$

$$= x_1(1 - x_1),$$

i.e., we have homogamy. Finally, the proof of homogamy for the case $\pi_{22} > \pi_{12} > \pi_{11}$ simply follows by switching the roles of π_{11} and π_{22} (and of x_1 and $1 - x_1$) in the previous case. $\qquad\square$

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