Sensitivity to Model Structure in a Stochastic Rosenzweig-MacArthur Model Driven by a Compound Poisson Process

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A Thesis Submitted to the School of Graduate Studies in the Partial Fulfillment of the Requirements for the Degree Masters of Science

Abstract

In this thesis we study the matter of hypersensitivity to model structure in the Rosenzweig-MacArthur predator-prey model, and in particular whether the introduction of stochasticity reduces the sensitivity of the ω-limit sets to small changes in the underlying vector field. To do this, we study the steady-state probability distributions of stochastic differential equations driven by a compound Poisson process on a bounded subset of $\mathbb{R}^n$, as steady-state distributions are analogous to ω-limit sets for stochastic differential equations. We take a primarily analytic approach, showing that the steady-state distributions are equivalent to weak measure-valued solutions to a certain partial differential equation. We then analyze perturbations of the underlying vector field using tools from the theory of compact operators. Finally, we numerically simulate and compare solutions to both the deterministic and stochastic versions of the Rosenzweig-MacArthur model.

Acknowledgements

I would first like to thank my supervisor, Professor Gail Wolkowicz, for introducing me to this topic, helping me formulate a coherent approach to the problem, providing advice, and helping me edit the final result. Our conversations frequently gave me new angles to consider and clarified my thinking.

I would also like to thank Professor Stan Alama and Professor Dmitry Pelinovsky for lending me their expertise on multiple occasions when I had difficult and obscure questions about analysis.

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Chapter 1

Introduction and Preliminaries

1.1 Background and Introduction

The general form of the classic Rosenzweig-MacArthur (R-M) predator-prey model is

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \Phi(N)P, \quad \frac{dP}{dt} = (\Phi(N) - m)P \tag{1.1.1}$$

where $N(t)$ is a measure of the prey population at time t and $P(t)$ is a measure of the predator population at time t. Each of the parameters r, m, and K appearing in this pair of equations has a biological interpretation. In the absence of predation, the prey population grows logistically, with r representing the maximum growth rate and K the maximum sustainable population. In the absence of prey, the predator population decreases exponentially at the rate m, which can therefore be interpreted as the death rate of the predator species. The parameter K is of greatest interest among these three due to its role in the "paradox of enrichment" [17], where under certain conditions a higher value for K can lead to large oscillations in $N(t)$ and $P(t)$ while a lower value results in convergence to a stable equilibrium.

Aside from the three scalar parameters r, m, K, the other unknown component of this model is the function $\Phi(N)$, which in the biological interpretation corresponds to the rate at which a single predator consumes prey given the current population N of prey. There have been multiple possible functions $\Phi(N)$ proposed for use in this model, including

$$\Phi_H(N) = \frac{a_H N}{1 + b_H N},$$

$$\Phi_I(N) = a_I(1 - e^{b_I N}),$$

$$\Phi_T(N) = a_T \tanh(b_H N).$$

We will refer to these functions as Holling type II, Ivlev, and Trigonometric respectively in order to be consistent with the terminology introduced in [10]. It should be noted that all three functions are classified as Holling type II according to the definition found in [12] since they vanish at zero, are non-decreasing, are concave down, and approach a finite limit as $N \to \infty$. Holling types I, III, and IV refer to other classes of uptake functions. Type I consists of linear functions, type III of functions that are concave up near zero but otherwise similar to type II, and type IV of functions that decrease for N sufficiently large but are otherwise similar to type II.

With suitable choices for the constants, these functions can be made extremely close to each other in the sense of the supremum norm. For example, if we set $a_I = 1, b_I = 1.5$ and $a_T = 1, b_T = 2$, we find that

$$\sup_{N \in \mathbb{R}^+} |\Phi_I(N) - \Phi_T(N)| \simeq 0.04.$$

Despite the similarity of the functions, the asymptotic behaviour of the dynamical system (1.1.1) depends strongly on exactly what form is chosen for Φ. For example, using the values $a_I = 1, b_I = 1.5$ and $a_T = 1, B_T = 2$, we have a stable equilibrium for $K < 10.116$ if Φ_T is the uptake function, while the equilibrium becomes unstable for $K > 1.071$ if we use Φ_I. This "hypersensitivity to model structure" was pointed out in [10], and represents a significant problem with the model as a reliable predictive tool.

We intend to determine the effect of adding a stochastic noise term to (1.1.1), and in particular whether the introduction of noise reduces the sensitivity of the long-term behaviour of the system to perturbations of the uptake function Φ. This approach is partially inspired by behaviour observed in the SIR model with vital dynamics, another important dynamical system defined by the differential equations

$$\frac{dS}{dt} = 1 - \mu S - \beta IS, \quad \frac{dI}{dt} = \beta IS - (\gamma + \mu)I. \tag{1.1.2}$$

This version of the SIR model is used to model the behaviour of disease epidemics over long periods of time. In this form the trajectories of the model (1.1.2) are very simple, having globally asymptotically stable equilibria as the only ω-limit sets. However, for certain parameter values, the introduction of even a small stochastic noise term dramatically alters the behaviour of the system, resulting instead in large-amplitude oscillations around the equilibrium. The papers [4] and [22] explore this feature of the SIR model in depth.

Given that this behaviour exists in the SIR model, we conjectured that stochastic noise could resolve the hypersensitivity issue by inducing oscillatory behaviour for parameter values where the deterministic model predicts convergence to an equilibrium.

To investigate the effects of noise, we will move to the more general setting of a Poisson-driven SDE on a domain $D \in \mathbb{R}^n$ as in [13]. This equation takes the form

$$dY(x,t) = b(Y(x,t)) + \int_\Theta j(Y(x,t),\theta)\omega(d\theta,dt), \; Y(x,0) = x, \tag{1.1.3}$$

where Θ is a measure space, ω is a Poisson point process on $\mathbb{R}^+ \times \Theta$ and $j(x,\theta)$ is a jump function $j : D \times \Theta \to \mathbb{R}^n$. The differential $dY(x,t)$ in (1.1.3) cannot be defined rigorously, since the process is discontinuous. Instead, this equation is shorthand for a certain integral equation that will be defined in the next section. We will show that the probability distribution of the process $Y(x,t)$ is a measure-valued weak solution of a PDE of the form

$$\partial_t \mu_t - \nabla \cdot (b\mu_t) - cA\mu_t + c\mu_t = 0 \tag{1.1.4}$$

where $c > 0$ is the rate of the Poisson process ω with respect to the time variable t, and A is a certain linear operator defined from the jump function $j(x, \theta)$. The precise definition of A will be introduced later.

Since SDEs do not have ω-limit sets is the usual sense, we focus instead on time-invariant probability distributions. Time-invariant probability distributions are analogous to ω-limit sets in that they represent the long-term behaviour of the SDE, after all transient effects resulting from the initial condition have decayed. Under appropriate conditions on the jump function $j(x, \theta)$, we will be able to prove that there exists a unique constant measure-valued solution μ_e to (1.1.4), and hence that there is a unique time-invariant probability distribution for $Y(x, t)$. Furthermore, we will be able to prove under reasonable assumptions that the solution μ_e is not arbitrarily sensitive to perturbations of b and A.

After proving this main result, we perform some numerical investigations of the Rosenzweig-MacArthur model with Poisson noise. The numerical approximations for the distribution μ that we compute indicate that although the noise term helps reduce the sensitivity, the difference in the steady state distributions resulting from $\Phi_I(N)$ and $\Phi_T(N)$ is still very significant. Therefore, the issue of hypersensitivity cannot be considered resolved, theoretically or computationally, by the addition of Poisson-driven stochastic noise.

1.2 Notation and Definitions

Throughout, λ will always refer to the Lebesgue measure on $\mathbb{R}^n$ and δ_x to the Dirac measure at the point x. If μ is a measure on the measurable space Ω and $K \subset \Omega$ is measurable, we denote the restriction of μ to K by $\mu|_K$.

We will focus on a single bounded domain $D \subset \mathbb{R}^n$ and define $Z := C^0(D)^*$. By the Riesz-Markov-Kakutani representation theorem, this space Z can be identified with the set of regular signed Borel measures on D, and the norm on Z corresponds to the total variation norm, which we write $||\cdot||_{TV}$.

We will also need to use the much larger space $W := BL(D)^*$, the dual of the space $BL(D)$ of bounded Lipschitz functions on D equipped with the norm

$$||f||_{BL(D)} = \max\{\sup_{x \in D} |f(x)|, L\}$$

where L is the Lipschitz constant of f. Because there is a natural inclusion of $I : C^0(D) \to BL(D)$, there is also a natural inclusion $I^* : Z \to W$. From now on we will not write this inclusion operator explicitly, and by a slight abuse of notation consider elements of Z as naturally also belonging to W.

The W-norm is a "natural" norm for the comparison of probability measures on $\mathbb{R}^n$, since unlike the total variation norm it incorporates the metric on the domain as well as the probabilities of events. However, the Banach space W also includes elements which are not measures, so we must take care not to assume that a general element of W corresponds to an element of Z.

Throughout this thesis, we will make use of integrals of functions from $\mathbb{R}$ to Z. Since Z is not separable, many Z-valued functions are not Bochner integrable. See the appendix of [9] for further discussion of Bochner integrability. For our purposes, it suffices to have the integral exist in a weak sense, so we make the following definition.

Definition 1.2.1. *Let $\mu_t : [0,T] \to Z$ be a Z-valued function. We say that μ_t is weakly measurable if $\forall f \in C^0(D),\ t \mapsto \langle f, \mu_t \rangle$ is Lebesgue measurable from $[0,T] \to \mathbb{R}$. If μ_t is weakly measurable and*

$$\int_0^T ||\mu_t||_{TV} dt < \infty,$$

then we can define a bounded linear functional g on $C^0(D)$ by

$$\forall f \in C^0(D),\ \langle g, f \rangle := \int_0^T \int_D f(x) d\mu_t,$$

since

$$\left| \int_0^T \int_D f(x) d\mu_t dt \right| \leq ||f||_{C^0} \int_0^T ||\mu_t||_{TV} dt.$$

Then $g \in Z$ and so we define

$$\int_0^T \mu_t = g.$$

Given a Lipschitz vector field b defined on the bounded domain $D \subset \mathbb{R}^n$ such that D is forward-invariant with respect to b, we define $X_b(x,t) : [0,\infty) \to D$ to be the unique flow starting at the point x along the vector field b. That is, $X_b(x,t)$ satisfies

$$X_b(x,t) = x + \int_0^t b(X_b(x,\tau)) d\tau,\ \forall x \in D, t \in \mathbb{R}.$$

As in [1], we introduce the pushforward operator $X_{b,t}^{\#} : W \to W$ defined by the identity

$$\langle v(x), X_{b,t}^{\#} \mu \rangle_{C^1} = \langle v(X_b(x,t)), \mu \rangle_{C^1}.$$

Chapter 2

The Poisson Driven Differential Equation

We begin by giving the precise definition of the Poisson random measure that will drive the stochastic component of the SDE (1.1.3). See [6] for a more general discussion of Poisson-driven stochastic differential equations.

Definition 2.1.1. *Let Θ be a measurable space and let G be a probability measure on Θ. The probability space Ω is defined to be the set of counting measures ω on $\mathbb{R}^+ \times \Theta$, and the probability measure $\mathbb{P}$ is the unique probability measure on Ω such that for all $K \in \mathbb{R}^+ \times \Theta$ measurable and with $[c\lambda \times G](K) < \infty$,*

$$\mathbb{P}(\omega(K) = n) = \frac{([c\lambda \times G](K))^n}{n!} e^{-[c\lambda \times G](K)}$$

and $\omega(K) = n$ is independent of $\omega(K') = m$ if $K \cap K' = \emptyset$. Additionally, let $\mathcal{F}_t$ be the filtration on Ω defined by $A \in \mathcal{F}_t$ if and only if $\forall \omega, \omega' \in \Omega$

$$\omega|_{[0,T]\times\Theta} = \omega'|_{[0,T]\times\Theta} \Rightarrow \omega, \omega' \in A \text{ or } \omega, \omega' \in A^c.$$

With these definitions, $(\Omega, \mathcal{F}_t, \mathbb{P})$ is a filtered probability space.

A proof that such a measure $\mathbb{P}$ exists and is unique can be found in chapter 3 of [14]. We can now give the rigorous definition of a solution to the Poisson-driven SDE (1.1.3). For each fixed $x \in D$, the process $Y(x, t, \omega) : \mathbb{R}^+ \times \Omega \to D$ adapted to $\mathcal{F}_t$ is defined to be a solution to (1.1.3) with initial condition x if it satisfies

$$Y(x, t, \omega) = x + \int_0^t b(Y(x, \tau, \omega))d\tau + \int_0^t \int_\Theta j(Y(x, \tau-, \omega), \theta)d\omega, \ \forall t \in \mathbb{R}^+ \tag{2.1.1}$$

$\mathbb{P}$-almost surely. Here $b(x)$ is a $C^1(D)$ vector field for which D is a forward-invariant set, and $j(x, \theta) : D \times \Theta \to \mathbb{R}^n$ is a jump function that depends on the current location of the process and on the measure space Θ. We make the following assumptions about j.

$$\begin{aligned} &\forall x \in D, \theta \in \Theta, \ x + j(x, \theta) \in D \\ &\exists \alpha, C > 0, \ |j(x, \theta) - j(y, \theta)| \leq C|x - y|^\alpha, \ \forall x, y \in D, \theta \in \Theta. \\ &\exists \sigma : D \times D \to \mathbb{R} : \int_\Theta f(x + j(x, \theta))dG(\theta) = \int_D \sigma(x, y) f(y)dy, \ \forall x \in D. \end{aligned} \tag{2.1.2}$$

The first of these assumptions is needed so that the endpoints of the jumps remain in the bounded domain D. The second ensures that the jump resulting from any point θ in the measure space Θ is at least α-Hölder continuous with respect to the position x for some α. Finally, we assume that this jump function admits an x-dependent density σ.

In the next proposition, we prove that a process $Y_\omega(x,t)$ satisfying (2.1.1) exists. From here on we will suppress the explicit dependence of $Y(x,t,\omega)$ on ω and simply write $Y(x,t)$.

Proposition 2.1.1. *For each $x \in D$ there is an $\mathcal{F}_t$-adapted process $Y(x,t) : \mathbb{R}^+ \to D$ satisfying (2.1.1) a.s. Furthermore, this process has the Markov property.*

Proof. Note that for any $T > 0$ the set $[0,T] \times \Theta$ has finite measure under $c\lambda \times G$, and therefore

$$\mathbb{P}(\omega([0,T] \times \Theta) < \infty) = 1.$$

Hence, after excluding a $\mathbb{P}$-null set, we may assume that $\omega|_{[0,T]\times\Theta}$ is supported on a countable set of points (t_i, θ_i), $i \in \mathbb{N}$ ordered so that $t_i < t_{i+1}$. Since the vector field $b(x)$ is Lipschitz and D is forward-invariant under $b(x)$, we can construct the unique flow $X_b(x,t)$. Then we define $Y(x,t)$ for $t \in [0,T]$ by

$$Y(x,t) =: \begin{cases} X(Y(x,s),t), \ t \in [0,t_0) \\ X(Y(x,t_i) + j(Y(x,t_i),\theta_i), t - t_i)), \ t \in [t_i, t_{i+1}). \end{cases} \tag{2.1.3}$$

By straightforward calculus the process (2.1.3) satisfies the integral equation (2.1.1) and is adapted. Furthermore, note that if $0 \le s < t$, then $Y(x,t)$ can be determined from only $\omega|_{[s,t]\times\Theta}$ and the value $Y(x,s)$, and hence the process is Markov. □

To prove that the density of the process (2.1.3) satisfies an equation of the type (1.1.4), we follow a martingale argument similar to those introduced in [19]. In the next proposition, we construct a martingale based on $f(Y(x,t),t)$ for any arbitrary function $f(x,t) \in C^1(D \times \mathbb{R}^+)$.

Proposition 2.1.2. *If $f(x,t) \in C^1(D \times \mathbb{R}^+)$ the $\mathcal{F}_t$-adapted process*

$$\Big\{ f(Y(x,t),t) - \int_0^t f_t(Y(x,\tau),\tau) + b(Y(x,\tau)) \cdot \nabla f(Y(x,\tau),\tau)) \\ + c\int_D \sigma(Y(x,\tau),y) f(y) dy - cf(Y(x,\tau),\tau)) d\tau, \mathcal{F}_t, \mathbb{P} \Big\} \tag{2.1.4}$$

is a martingale.

Proof. We fix times s,t with $0 \le s < t$ and assume $t - s < 1$. Throughout this proof we assume, by excluding a $\mathbb{P}$-null set, that $\omega([s,t) \times \Theta) < \infty$. Under these circumstances the process $Y(x,t)$ is piecewise differentiable and so it follows by elementary calculus that

$$f(Y(x,t),t) = f(Y(x,s),s) + \int_s^t f_t(Y(x,\tau),\tau) + b(Y(x,\tau)) \cdot \nabla f(Y(x,\tau),\tau))d\tau$$
$$+ \int_s^t \int_\Theta f(Y(x,\tau-) + j(Y(x,\tau-),\theta),\tau) - f(Y(x,\tau-),\tau))d\omega(\tau,\theta) \quad (2.1.5)$$

almost surely. Therefore, it suffices to show that

$$\mathbb{E}\Big[\int_s^t \int_\Theta f(Y(x,\tau-) + j(Y(x,\tau-),\theta),\tau) - f(Y(x,\tau-),\tau))d\omega \Big| Y(x,s)\Big]$$
$$= c\int_D \sigma(Y(x,\tau),y)f(y)dy - cf(Y(x,\tau),\tau))d\tau.$$

Define the random variable

$$T_0(\omega) = \begin{cases} \sup\{r \in [s,t) : \omega([s,r) \times \Theta) = 0\}, \text{ if } \omega([s,t) \times \Theta) = 1, \\ t \text{ otherwise.} \end{cases}$$

Applying Grönwall's inequality, if $T_0 < t$ we have

$$|Y(x,T_0-) - Y(x,s)| \le C(t-s)$$

where C depends only on b, since $Y(x,T_0-) = X_b(Y(x,s),T_0-s)$, and hence if $T_0 < t$ we have

$$|f(Y(x,T_0-) + j(Y(x,T_0-),\theta)) - f(Y(x,s) + j(Y(x,s),\theta))|$$
$$\le C(t-s)^\alpha, \ \forall \theta \in \Theta, \quad (2.1.6)$$

where C depends on b, j, f and α is in (2.1.2). From this we get, $\forall r \in [s,t)$,

$$\Big|\mathbb{E}\Big[\int_s^t \int_\Theta f(Y(x,\tau-) + j(Y(x,\tau-),\theta),\tau) - f(Y(x,\tau-),\tau))d\omega \Big| Y(x,s), T_0 = r\Big]$$
$$- \int_\Theta f(Y(x,s) + j(Y(x,s),\theta))dG(\theta)\Big| \le C(t-s)^\alpha. \quad (2.1.7)$$

Note that $\mathbb{P}(\omega([s,t) \times \Theta) > 1) \le C(t-s)^2$ for some $C > 0$, and also $|\mathbb{P}(\omega([s,t) \times \Theta) = 1) - c(t-s)| \le C(t-s)^2$. By the law of total probability, we obtain

$$\Big|\mathbb{E}\left[\int_s^t \int_\Theta f(Y(x,\tau-) + j(Y(x,\tau-),\theta),\tau) - f(Y(x,\tau-),\tau))d\omega(\tau,\theta) \Big| Y(x,s)\right]$$
$$-(t-s)\int_\Theta f(Y(x,s) + j(Y(x,s),\theta))dG(\theta)\Big| \le C(t-s)^{1+\alpha}. \quad (2.1.8)$$

We can now partition the interval $[s,t)$ into N subintervals $[s_i, s_{i+1})$ of maximum length B, and write

$$\begin{aligned}\mathbb{E}\left[\int_s^t \int_\Theta f(Y(x,\tau-)+j(Y(x,\tau-),\theta),\tau) - f(Y(x,\tau-),\tau))d\omega(\tau,\theta)\middle|Y(x,s)\right] \\ = \sum_{i=1}^{N}\mathbb{E}\bigg[\int_{s_i}^{s_{i+1}}\int_\Theta f(Y(x,\tau-)+j(Y(x,\tau-),\theta),\tau) \\ - f(Y(x,\tau-),\tau))d\omega(\tau,\theta)\bigg|Y(x,s)\bigg]. \quad (2.1.9)\end{aligned}$$

By the tower property of conditional expectation, the Markov property for $Y(x,s)$, and (2.1.8), we have

$$\begin{aligned}\bigg|\mathbb{E}\bigg[\int_{s_i}^{s_{i+1}}\int_\Theta f(Y(x,\tau-)+j(Y(x,\tau-),\theta),\tau) \\ - f(Y(x,\tau-),\tau))d\omega(\tau,\theta)\bigg|Y(x,s)\bigg] \\ -(s_{i+1}-s_i)\mathbb{E}\left[\int_\Theta f(Y(x,s_i)+j(Y(x,s_i),\theta))dG(\theta)\middle|Y(x,s)\right]\bigg| \\ \leq C(s_{i+1}-s_i)^{1+\alpha}. \quad (2.1.10)\end{aligned}$$

Observing that the function

$$s_i \mapsto \mathbb{E}\left[\int_\Theta f(Y(x,s_i)+j(Y(x,s_i),\theta))dG(\theta)\middle|Y(x,s)\right]$$

is Riemann integrable and using the third assumption from (2.1.2), we have the result. □

Before continuing, we define the bounded operator A^* acting on $f(x) \in C^0(D)$ by

$$[A^*f](x) = \int_\Theta f(x+j(x,\theta))d\theta = \int_D \sigma(x,y)f(y)dy.$$

We require that $\sigma(x,y)$ satisfies the following set of conditions

$$\begin{aligned}&\forall x,y\in D,\ \sigma(x,y)\geq 0 \\ &\forall x\in D,\ \int_D \sigma(x,y)dy = 1 \\ &\forall x\in D,\ \sigma(x,\cdot)\in C^1(D) \\ &\exists B>0 : \forall x\in D,\ ||\sigma(x,\cdot)||_{C^1(D)}< B \\ &\sigma(x,\cdot): D\to Z \text{ is Lipschitz.} \\ &\forall E \text{ open},\ E\neq\emptyset,\ E\subset D,\ \int_E\int_{D\setminus E}\sigma(x,y)dxdy>0.\end{aligned} \quad (2.1.11)$$

The first two conditions here follow immediately from the definition of σ. The third, fourth, and fifth are smoothness assumptions, ensuring that the distribution of the jumps the process makes has reasonably regular dependence on the current state of the process. The final assumption guarantees that there are no boundaries in the domain which the process cannot "jump across". These assumptions are easily satisfied by most natural choices of jump function for biological models.

We are now prepared to prove the main result of this section, establishing the relationship between weak solutions to the PDE (1.1.4) and the stochastic process $Y(x,t)$.

Proposition 2.1.3. *Assume that $\mu_{x,t} : D \times \mathbb{R}^+ \to Z$ is a Z-valued function that satisfies the equation*

$$\int_0^T \int_D (\partial_t + b(x) \cdot \nabla + cA^* - c) f(x,t) d\mu_{x,t} dt = -f(x,0) \tag{2.1.12}$$

for all $f(x,t) \in C^1([0,T] \times D)$ with $f(x,T) = 0$. Then, $\mu_{x,t} \in \mathcal{M}(D)$ satisfies

$$\mathbb{E}[h(Y(x,t))] = \int_D h d\mu_{x,t} \tag{2.1.13}$$

for any $h \in C^0(D)$.

Proof. For each $(x,t) \in D \times \mathbb{R}^+$ define $\mu_{x,t}$ to be the unique element of Z satisfying the identity (2.1.13) for each $h \in C^0(D)$. Let f be any $C^1(D \times [0,T])$ function with $f(x,T) = 0$. Then by Fubini's theorem and Proposition 2.1.2 we get

$$\begin{aligned}\mathbb{E}\Big[f(Y(x,T),T) - \int_0^T & f_t(Y(x,t),t) + b(Y(x,t)) \cdot \nabla f(Y(x,t),t)) \\ &+ \int_D \sigma(Y(x,t),y) f(y) dy - cf(Y(x,t),t)) dt\Big] \\ &= -\int_0^T \int_D (\partial_t + b(x) \cdot \nabla + cA^* - c) f(x,t) d\mu_{x,t} dt = f(x,0).\end{aligned} \tag{2.1.14}$$

On the other hand, we show in the appendix that the Z-valued solution of (2.1.12) is unique, which gives the result. □

To summarize this section, we have proven that the unique weak solution of (2.1.12) allows us to compute expectation values of $\mathbb{E}[h(Y(x,t))]$ for all $C^0(D)$ functions $h(x)$.

Chapter 3

Stability of Steady State Probability Distributions

3.1 Existence and Uniqueness of Steady States

We mentioned in the introduction that time-invariant probability distributions were analogous to ω-limit sets for SDEs. Therefore, our objective now is to investigate the time-invariant solutions of the equation

$$\int_0^T \int_D (\partial_t + b(x) \cdot \nabla + cA^* - c)v(x,t)d\mu_t dt + \int_D v(x,0)d\mu_0 = 0,$$
$$\forall v(x,t) \in C^1(D \times [0,T]) : v(x,T) = 0, \quad (3.1.1)$$

where A is the linear convolution operator introduced in the previous section, b is a Lipschitz vector field, and $c \in \mathbb{R}^+$. Before constructing solutions μ_t to (3.1.1) we must develop some preliminary results.

Recall that we defined $X_b(x,t)$ to be the flow associated with b and $X^\#_{b,t}$ the pushforward operator associated with the flow $X_b(x,t)$. Observe that if $\mu \in Z$, then $||X^\#_{b,t}\mu||_{TV}= ||\mu||_{TV}$. The next equation summarizes some properties of solutions to (3.1.1).

Proposition 3.1.1. *A weakly measurable Z-valued function $\mu_t : \mathbb{R}^+ \to Z$ satisfies (3.1.1) $\forall T > 0$ if and only if μ_t satisfies*

$$\mu_t = e^{-ct} X^\#_{b,t}\mu_0 + \int_0^t e^{-c(t-\tau)} X^\#_{t-\tau} A\mu_\tau d\tau, \ \forall t > 0 \quad (3.1.2)$$

where the integral in the expression (3.1.2) is taken in the sense of (1.2.1). Furthermore, for each μ_0 there exists a unique such μ_t, and μ_t satisfies

$$||u_t||_{TV} \leq ||u_0||_{TV}, \ \forall t \in \mathbb{R}^+, \quad (3.1.3)$$

and

$$\int_D 1 d\mu_t = \int_D 1 d\mu_0, \ \forall t \in \mathbb{R}^+. \quad (3.1.4)$$

Finally, the solution satisfies a semigroup property. That is, if μ_t is a solution and $\hat{\mu}_t$ is another solution with initial data $\hat{\mu}_0 = \mu_s$ for some $s > 0$, then $\hat{\mu}_r = \mu_{s+r}$ $\forall r > 0$.

The proof of this proposition is long and mostly straightforward, so we have placed it in the appendix.

Before proceeding to construct the steady state solutions, we must prove some results on the operator A that follow from (2.1.11). We begin with a lemma.

Lemma 1. *Given any $\mu \in Z$, there is a sequence of measures μ_n, where each μ_n is a finite linear combination of point measures, such that $||\mu_n||_{TV} \leq ||\mu||_{TV}$, and $\lim_{n\to\infty} ||\mu - \mu_n||_W = 0$.*

Proof. For any n, we can partition D into a finite number N of disjoint sets S_i such that $\operatorname{diam}(S_i) \leq 1/n$. For each S_i, choose an arbitrary point $x_i \in S_i$. We then define

$$\mu_n =: \sum_{i=0}^{N} \mu(S_i)\delta_{x_i}.$$

It is clear that $||\mu_n||_{TV} \leq ||\mu||_{TV}$. Define a measure ν_i by $\nu_i(E) = \mu(E \cap S_i)$, and observe that

$$||\nu_i - \mu(S_i)\delta_{x_i}||_W = \sup_{||f||_{BL(D)}=1} \int_{S_i} f d\mu - \mu(S_i) f(x_i) \leq \frac{1}{n} ||\nu_i||_{TV},$$

since any such f satisfies $\sup_{x\in S_i} |f(x) - f(x_i)| \leq 1/n$. Since $\sum \nu_i = \mu$, we have

$$||\mu - \mu_n||_W \leq \sum_{i=0}^{N} ||\nu_i - \mu(S_i)\delta_{x_i}||_W \leq \frac{1}{n} \sum_{i=0}^{N} ||\nu_i||_{TV} = \frac{1}{n} ||\mu||_{TV}.$$

□

We are now ready to prove the main properties of A.

Proposition 3.1.2. *If $\sigma(x,y)$ satisfies (2.1.11), and L is the Lipschitz constant associated with the map $\sigma(x,\cdot) : D \to L^1(D)$, then*

$$\forall \mu \in Z, \; ||A\mu||_{TV} \leq L||\mu||_W. \tag{3.1.5}$$

Furthermore, for all $\mu \in Z$, the measure $A\mu$ is absolutely continuous with respect to the Lebesgue measure on D and its Radon-Nikodym derivative is a continuous function.

Proof. Let $v \in C^0(D)$ satisfy $||v||_{C^0} = 1$. By the fifth assumption in (2.1.11),

$$[A^*v](x) = \int_D \sigma(x,y)v(y)dy$$

is a Lipschitz function of x with Lipschitz constant L. Then it is clear that

$$\int_D v(y) dA\mu(y) = \int_D \int_D \sigma(x,y)v(y)dyd\mu(x) \leq L||\mu||_W,$$

which suffices to conclude (3.1.5). To prove the second part, we define μ_n as Lemma (1), and observe by the third and fourth assumptions in (2.1.11) that $A\mu_n \ll \lambda$ and

$$\left|\left|\frac{dA\mu_n}{d\lambda}\right|\right|_{C^1} \leq B||\mu||_{TV}.$$

By the Arzela-Ascoli theorem, there must be a subsequence μ_{n_k} and a continuous function u such that

$$\left|\left|\frac{dA\mu_{n_k}}{d\lambda} - u\right|\right|_{C^0} \to 0.$$

Since

$$||A\mu - A\mu_n||_{TV} \leq L||\mu - \mu_n||_W,$$

we conclude that $A\mu = u\lambda$. □

Corollary 1. *Since Z is dense in W, A extends uniquely to a bounded linear map $W \to Z$.*

In order to obtain steady state solutions, we introduce a linear operator $\omega : Z \to Z$ defined by

$$\int_D f d\omega(\mu_0) = \lim_{s\to\infty} \frac{1}{s} \int_0^s \int_D f d\mu_s ds.$$

The following proposition collects some properties of ω that we will need.

Proposition 3.1.3. *For any $\mu_0 \in Z$, $\omega(\mu_0)$ is a constant solution of (3.1.1), and $\omega(\mu_0) = \mu_0$ if μ_0 is a constant solution of (3.1.1). Furthermore, $\omega(\mu_0) \ll \lambda$ and $\frac{d\omega(\mu_0)}{d\lambda} \in C^0(D)$, and*

$$\int_D 1 d\mu_0 = \int_D 1 d\omega(\mu_0).$$

Finally, if $\mu_0 \geq 0$, then $\omega(\mu_0) \geq 0$ and $\omega(\mu_0)(E) > 0$ for each open set $E \subset D$.

Proof. By the semigroup property of solutions to (3.1.1), given any solution μ_t with initial data μ_0 to (3.1.1) and any $s > 0$, the measure

$$\nu_t^s =: \frac{1}{s}\int_0^s \mu_{t+\tau} d\tau$$

satisfies

$$\int_0^T \int_D (\partial_t + b(x)\cdot\nabla + cA^* - c)v(x,t)d\nu_t^s dt$$
$$= \frac{1}{s}\int_0^s \int_0^T \int_D (\partial_t + b(x)\cdot\nabla + cA^* - c)v(x,t)d\mu_{t+\tau}dt$$
$$= -\frac{1}{s}\int_0^s \int_D v(x,0)\mu_\tau d\tau = -\int_D v(x,0)d\nu_0^s.$$

Additionally, note that

$$||\nu_{t+r}^s - \nu_t^s||_{TV} \leq \frac{1}{s}\left|\left|\int_t^{t+r}\mu_\tau d\tau\right|\right|_{TV} + \frac{1}{s}\left|\left|\int_{t+s}^{t+s+r}\mu_\tau d\tau\right|\right|_{TV} \leq \frac{2r}{s},$$

so it is clear that

$$\begin{aligned}\int_0^T\int_D(\partial_t + b(x)\cdot\nabla + cA^* - c)v(x,t)d\omega(\mu_0)dt \\ = \lim_{s\to\infty}\int_0^T\int_D(\partial_t + b(x)\cdot\nabla + cA^* - c)v(x,t)d\nu_t^s dt \\ = \lim_{s\to\infty} -\int_D v(x,0)d\nu_0^s = -\int_D v(x,0)d\omega(\mu_0),\end{aligned}$$

and hence $\omega(\mu_0)$ is indeed a steady state solution. By Proposition 3.1.1, this implies that

$$\omega(\mu_0) = e^{-ct}X_{b,t}^{\#}\omega(\mu_0) + \int_0^t e^{-c\tau}X_{b,\tau}^{\#}A\omega(\mu_0)d\tau, \ \forall t > 0.$$

We can also take the limit $t \to \infty$ in this expression to obtain

$$\omega(\mu_0) = \int_0^\infty e^{-c\tau}X_{b,\tau}^{\#}A\omega(\mu_0)d\tau, \tag{3.1.6}$$

from which we can conclude that $\omega(\mu_0) \ll \lambda$ with continuous Radon-Nikodym derivative.

The map ω is positivity-preserving, as can be easily seen from the fact that $\mu_t \geq 0$ for $\mu_0 \geq 0$. Additionally,

$$\int_D 1d\omega(\mu_0) = \lim_{s\to\infty}\frac{1}{s}\int_0^s\int_D 1d\mu_\tau d\tau = 1.$$

Let E^* be the union of all open sets $E \subset D$ such that $[\omega(\mu_0)](E) = 0$. Since $\omega(\mu_0) \geq 0$ and $\omega(\mu_0) \neq 0$, if $E^* \neq \emptyset$, we have

$$[A\omega(\mu_0)](E^*) = \int_{E^*}\int_{D\setminus E^*}\sigma(x,y)d\omega(\mu_0)dy > 0,$$

by the last assumption in (2.1.11). The function

$$\tau \mapsto [e^{-c\tau}X_{b,\tau}^{\#}A\omega(\mu_0)](E^*)$$

is continuous, non-negative, and not identically zero, and since

$$[\omega(\mu_0)](E^*) = \int_0^\infty [e^{-c\tau}X_{b,\tau}^{\#}A\omega(\mu_0)](E^*)d\tau,$$

we obtain a contradiction to the claim that $[\omega(\mu_0)](E^*) = 0$. □

We are now ready to prove the main theorem of this section, proving that time-independent solutions to 3.1.1 are unique up to a scaling constant.

Theorem 1. *For any $\mu_1, \mu_2 \in Z$, the images $\omega(\mu_1), \omega(\mu_2)$ are linearly dependent.*

Proof. Suppose that a measure $\nu \in Z$ satisfies $\nu = \omega(\nu)$. We take the Hahn-Jordan decomposition of ν to write $\nu = \nu^+ - \nu^-$ and we suppose that ν^+ and ν^- are both not identically zero. Since ν is in the image of ω, we have that the Radon-Nikodym derivative of ν with respect to λ exists and is a continuous function, and therefore that there is some open set $E \in D$ such that $\nu^-(E) = 0$ and $\nu^+(E) > 0$. We write

$$\nu(E) = \nu^+(E) = [\omega(\nu^+)](E) > [\omega(\nu^+)](E) - [\omega(\nu^-)](E) = [\omega(\nu)](E),$$

yielding a contradiction. Now let μ_1, μ_2 be two measures satisfying $\mu_i = \omega(\mu_i)$. Choose $C \in \mathbb{R}$ such that

$$\int_D 1 d(\mu_1 + C\mu_2) = 0.$$

Either $\mu_1 + C\mu_2 = 0$, in which case $\omega(\mu_1) + C\omega(\mu_2) = 0$ by linearity of ω, or $\mu_1 + C\mu_2$ has both positive and negative parts, in which case the preceding discussion leads to a contradiction. □

We are now able to define a measure μ_e as the unique non-zero element of the image of ω normalized so that

$$\int_D 1 d\mu_e = 1,$$

and the operator ω is a projection onto the one-dimensional space spanned by μ_e.

3.2 The Inhomogeneous Problem in W

To treat perturbations of the invariant solution u_e obtained in the previous section, we must consider the inhomogeneous problem

$$\mu = \int_0^\infty e^{-c\tau} X^{\#}_{b,\tau} A\mu d\tau + \nu \tag{3.2.1}$$

where ν is an arbitrary element of W, the dual space of Lipschitz functions on D, and μ is a solution belonging to the same space. To shorten notation, we introduce an operator S acting on W by

$$S\mu = \int_0^\infty e^{-c\tau} X^{\#}_{b,\tau} A\mu d\tau. \tag{3.2.2}$$

This integral is well-defined as a Bochner integral because W is separable and $t \mapsto e^{-ct} X^{\#}_{b,t} A\mu$ is continuous from $\mathbb{R}^+ \to W$. See [18] for more details on Bochner integrability. The first step toward solving (3.2.1) is to prove that this operator S is compact under the conditions (2.1.11) on A.

Proposition 3.2.1. *For any $f \in C^0(D)$, the operator $S : W \to W$ satisfies $|\langle S\mu, f\rangle| \leq C||\mu||_W ||f||_{C^0}$. Therefore for any $\mu \in W$, we can identify $S\mu$ with a measure in Z. Furthermore, S is compact from $W \to W$.*

Proof. Using the estimate 3.1.5 we find that $||X^{\#}_{b,t}A\mu||_{TV} = ||A\mu||_{TV} \leq L||\mu||_W$, so it follows by elementary calculus that

$$\langle S\mu, f\rangle = \int_0^\infty e^{-c\tau}\langle X^{\#}_{b,\tau}A\mu, f\rangle d\tau \leq \frac{L}{c}||\mu||_W||f||_{C^0}.$$

By the Arzela-Ascoli theorem, the inclusion operator $BL \to C^0(D)$ is compact, and by Schauder's theorem the adjoint of this inclusion operator is compact. It follows that the space $Z = C^0(D)^*$ is compactly embedded in the space W, and combining this with that fact that

$$||S\mu||_{TV} \leq \frac{L}{c}||\mu||_W,$$

we conclude that S is compact from W to itself. □

Having proven compactness, we are ready to use Fredholm theory to give necessary and sufficient conditions for a solution of (3.2.1) and obtain a bound on the W norm of the solutions.

Theorem 2. *Let $\nu \in W$ satisfy $\langle 1, \nu\rangle_{BL} = 0$. Then a unique solution μ to (3.2.1) exists with $||\mu||_W \leq C||\nu||_W$.*

Proof. Let $\mu \in W$ be a solution of

$$\mu - S\mu = 0.$$

By Proposition 3.2.1, $S\mu$ can be identified with an element of Z and hence we must have that $\mu \in Z$ as well. By Theorem 1, the space of such solutions in Z to $\mu - S\mu = 0$ has dimension one. Since S is compact, $I - S$ is a Fredholm operator and hence

$$\mu - S\mu = \nu$$

is solvable for $\nu \in W$ if and only if ν is orthogonal to the null space of $I - S^*$, and this null space must be one-dimensional as well [7]. It is easy to check that the constant function 1 is in the null space of $I - S^*$, so the orthogonality condition $\langle 1, \nu\rangle_{BL} = 0$ is a necessary and sufficient condition for the inhomogeneous problem to have a solution, and for some $C > 0$, we have $||\mu||_W \leq C||\nu||_W$ □

Next, we look at the stability of the unique steady-state solutions with respect to perturbations of both the vector field b and the linear operator A. In other words, if u_e is the unique normalized constant solution of (3.1.2), and $\hat{u}_e$ is the unique normalized constant solution of

$$\mu_t = e^{-ct}\hat{X}^{\#}_{b,t}\mu_0 + \int_0^t e^{-c(t-\tau)}\hat{X}^{\#}_{t-\tau}\hat{A}\mu_\tau d\tau, \ \forall t > 0, \tag{3.2.3}$$

where $X_{\hat{b}}(x,t)$ is the flow associated with $\hat{b} \in C^1(D)$, we are seeking a bound on $||u_e - \hat{u}_e||_W$ in terms of $c, b, \hat{b}$ and $A, \hat{A}$.

Theorem 3. *Assume that $\hat{u}_e$ is a solution of (3.2.3) normalized so $||\hat{u}_e||_{TV}= 1$, and that $\hat{A}$ is a bounded map from $W \to Z$. Let L be the Lipschitz constant associated with b, and let $||b-\hat{b}||_{L^\infty}< 1$. Then, if $c > L$,*

$$||u_e - \hat{u}_e||_W \leq C_1||b-\hat{b}||_{L^\infty} + C_2||A-\hat{A}||_{op(Z,Z)}.$$

If $c = L$,

$$||u_e - \hat{u}_e||_W \leq C_1||b-\hat{b}||_{L^\infty} \log(||b-\hat{b}||_{L^\infty})^2 + C_2||b-\hat{b}||_{L^\infty} + C_3||A-\hat{A}||_{op(Z,Z)}.$$

Finally, if $c < L$, we define

$$\alpha = \left(1 + \frac{c}{L-c}\right)^{-1},$$

then

$$||u_e - \hat{u}_e||_W \leq -C_1||b-\hat{b}||_{L^\infty}^{1-\alpha} \log(||b-\hat{b}||_{L^\infty}) + C_2||b-\hat{b}|| + C_3||A-\hat{A}||_{op(Z,Z)}.$$

All constants C_i are positive and depend only on b, c, A.

Proof. We define $\rho =: u_e - \hat{u}_e$ and observe that ρ satisfies

$$\rho = \int_0^\infty e^{-c\tau} X^\#_{b,\tau} A\rho + \nu \tag{3.2.4}$$

where

$$\nu = \int_0^\infty e^{-c\tau} \left[X^\#_{b,\tau}(A-\hat{A})\hat{u}_e + (X^\#_{b,\tau} - \hat{X}^\#_{b,\tau})\hat{A}\hat{u}_e\right] d\tau.$$

We see that the equation (3.2.4) is identical to the inhomogeneous problem (3.2.1). Therefore to estimate the difference $||\rho||_W$, it suffices to estimate $||\nu||_W$. We note that the first term in ν satisfies

$$\left|\left|\int_0^\infty e^{-c\tau} X^\#_{b,\tau}(cA - c\hat{A})\hat{u}_e d\tau\right|\right|_W \leq ||A-\hat{A}||_{op(Z,Z)},$$

since $||\hat{u}||_{TV}= 1$. Bounding the second term is slightly more complex. Since the W norm is weaker than the TV norm and the operator $X^\#_{b,t}$ preserves total variation, we have

$$||(X^\#_{b,\tau} - X^\#_{\hat{b},\tau})c\hat{A}\hat{u}_e||_W \leq ||(X^\#_{b,\tau} - \hat{X}^\#_{b,\tau})c\hat{A}\hat{u}_e||_{TV} \leq 2c. \tag{3.2.5}$$

In addition,

$$||(X^\#_{b,\tau} - \hat{X}^\#_{b,\tau})\hat{A}\hat{u}_e||_W \leq c||b-\hat{b}||_{L^\infty} \tau e^{L\tau}, \tag{3.2.6}$$

which can be proved using Grönwall's inequality as in Lemma 3.8 of [11]. To shorten the notation, we define

$$J =: \int_0^\infty e^{-c\tau}(X^\#_{b,\tau} - \hat{X}^\#_{b,\tau})\hat{A}\hat{u}_e.$$

Assume first that $L < c$. Then using (3.2.6) to write

$$||J||_W \leq \int_0^\infty ||b - \hat{b}||_{L^\infty} \tau e^{-(c-L)\tau} \hat{A}\hat{u}_e d\tau,$$

we get the first result. If $L = c$, we set $\beta = \frac{1}{c}\log(||b - \hat{b}||_{L^\infty})$ and divide the integral J into

$$\begin{aligned} ||J||_W \leq & \int_0^\beta ||b - \hat{b}||_{L^\infty} \tau d\tau + \int_\beta^\infty 2e^{-c\tau} d\tau \\ & \leq C_1 ||b - \hat{b}||_{L^\infty} \log(||b - \hat{b}||_{L^\infty})^2 + C_2 ||b - \hat{b}||_{L^\infty}, \end{aligned}$$

where we used (3.2.6) to estimate the first term and (3.2.5) to estimate the second. Finally, the argument for $L > c$ is similar to the case $L = c$. Setting

$$\beta = \frac{-\alpha \log(||b - \hat{b}||_{L^\infty})}{L - c},$$

we get

$$\begin{aligned} ||J||_W \leq & \int_0^\beta ||b - \hat{b}||_{L^\infty} \tau e^{(L-c)\tau} d\tau + \int_\beta^\infty 2e^{-c\tau} d\tau \\ & \leq -C_1 ||b - \hat{b}||_{L^\infty}^{1-\alpha} \log(||b - \hat{b}||_{L^\infty}) + C_2 ||b - \hat{b}||_{L^\infty}, \end{aligned} \quad (3.2.7)$$

where $C_1, C_2 > 0$. Furthermore, it is clear that $\langle 1, \nu \rangle_{BL} = 0$ and so by Theorem 2 we get the result. □

Chapter 4

Numerical Analysis of a Stochastic Rosenzweig-MacArthur Model

Now we return to the particular case of the Rosenzweig-MacArthur model to numerically investigate the sensitivity of the predator-prey system with respect to perturbations. In particular, we will focus on the different behaviours exhibited by the Ivlev and Trigonometric uptake functions. Recall that these functions are defined by

$$\Phi_I(N) = 1 - e^{-2N},\ \Phi_T(N) = \tanh(1.5N)$$

and note that $\sup_{N\in\mathbb{R}^+}|\Phi_I(N) - \Phi_T(N)| \simeq 0.04$. We then define a family of vector fields on D parameterized by $\gamma \in [0,1]$ by

$$b_\gamma(N,P) = \begin{bmatrix} rN\left(1 - \frac{N}{K}\right) - (\gamma\Phi_T(N) + (1-\gamma)\Phi_I(N))P \\ ((\gamma\Phi_T(N) + (1-\gamma)\Phi_I(N) - m)P. \end{bmatrix} \tag{4.1.1}$$

From this point on, we fix $K = 3$, $m = 1.48$, $r = 1$. The region $[0,3]^2$ is a forward invariant set for all the vector fields b_γ for $\gamma \in [0,1]$, so we define $D = [0,3]^2$. If no stochastic term is included, we find that for K, r, m fixed at these values, $\gamma = 0$ results in a periodic orbit and $\gamma = 1$ results in a stable equilibrium, with a bifurcation occurring near $\gamma = 0.34$.

In order to numerically model the stochastic version, we must make a particular choice of jump function $j(x,\theta)$. We choose $\Theta = [0,1]^2$ and $G = \lambda$, and then set

$$j(N,P,\theta) = (M(N) + \eta(N+0.1)\phi(\theta_1), M(P) + \eta(P+0.1)\phi(\theta_2))$$

where $\phi : [0,1] \to [0,1]$ and $\forall x \in [0,3]$, $M(x)+x+(x+0.1)\eta < 3$ and $M(x)+x > 0$. This form of j is chosen so that size of the jumps in either population is roughly proportional to the population size, and the size of the jumps in the predator population and prey populations are independent. We choose ϕ such that $\phi \circ d\lambda = 30x^2(1-x^2)d\lambda$.

One can check that $||b_T||_{C^1} < 12$ and $||b_I||_{C^1} < 12$, so by setting the jump frequency parameter as $c = 12$ we guarantee that the system is in the first case, $c > L$, from Theorem 3.

Now suppose that $\mu_{\gamma,c}$ is the unique steady state solution of

$$\partial_t \mu_t - \nabla \cdot (b_\gamma \mu_t) - cA\mu_t + c\mu_t = 0. \tag{4.1.2}$$

We next define an approximation to $\mu_{\gamma,c}$ that is convenient for numerical calculations.

Definition 4.1.1. *Consider the stochastic process $Y_{\gamma,c}(x,t)$ satisfying*

$$Y(x,t,\omega) = x + \int_0^t b_\gamma(Y(x,\tau,\omega))d\tau + \int_0^t \int_\Theta j(Y(x,\tau-,\omega),\theta)d\omega,\ \forall t \in \mathbb{R}^+$$

and let $y_{\gamma,c}(t)$ be a single realization of this process. Furthermore, let t_i, $0 \le i \le N$ be an increasing sequence of times in $[0,T]$ and let x_j, $0 \le j \le M$ be a finite collection of points in D, and for any $x \in D$ define $Q(x)$ to be $\operatorname{argmin}_{x_j}|x - x_j|$. We define the approximate steady state measure $\tilde{\mu}_e$ by

$$\tilde{\mu}_{\gamma,c} =: \frac{1}{N}\sum_{i=0}^{N} \delta_{Q(y_{\gamma,c}(t_i))}.$$

Equivalently, this defines a set of coefficients α_j, $0 \le j \le M$ such that

$$\tilde{\mu}_{\gamma,c} = \sum_{j=0}^{M} \alpha_j \delta_{x_j}. \tag{4.1.3}$$

This form of $\tilde{\mu}_{\gamma,c}$ is usually the most convenient to use.

We use an evenly-spaced grid on $[0,3]^2$ as the set of points x_j, and evenly-spaced time steps for the times t_i.

Figures 4.1 and 4.2 show the densities of the approximate solutions for various γ values, with and without stochasticity. Note that a similar change occurs over a much smaller range of γ values when the stochasticity is removed.

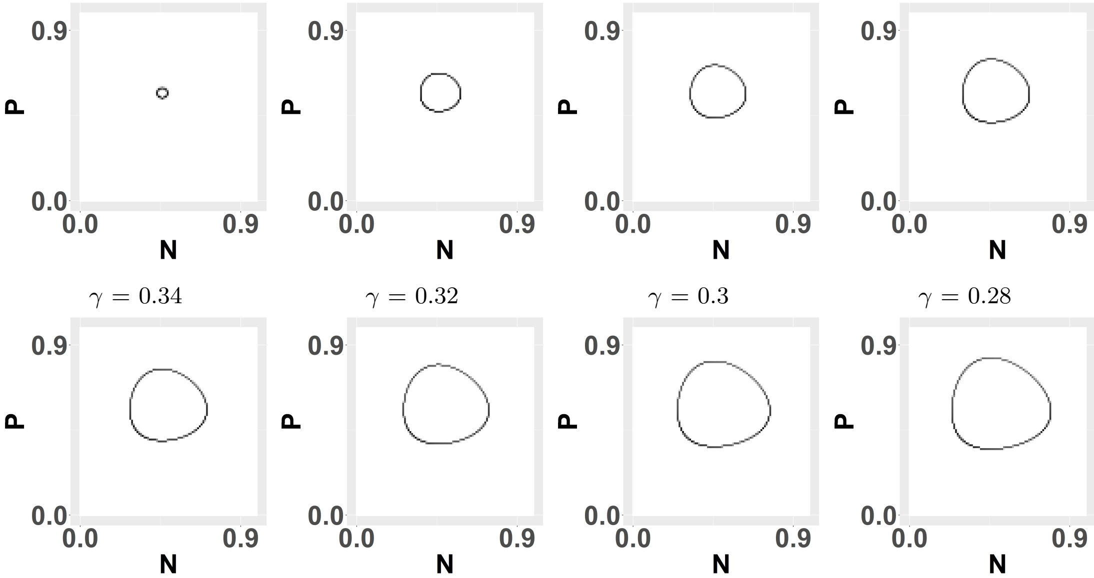
We then repeat this numerical process with a new parameterized family of vector fields, this time interpolating between the Ivlev and Holling type II uptake functions. We use

$$\Phi_H(N) = \frac{3.05N}{1 + 2.68N}$$

and this time we have $\sup_{N\in\mathbb{R}^+}|\Phi_I(N) - \Phi_H(N)| \simeq 0.06$. We then define a family of vector fields on D parameterized by $\nu \in [0,1]$ by

$$b_\nu(N,P) = \begin{bmatrix} rN\left(1 - \frac{N}{K}\right) - (\nu\Phi_H(N) + (1-\nu)\Phi_I(N))P \\ ((\nu\Phi_H(N) + (1-\nu)\Phi_I(N) - m)P. \end{bmatrix} \tag{4.1.4}$$

Figures 4.3 and 4.4 show the densities of the approximate solutions for various ν values, with and without stochasticity. In figure 4.2, we can see at $\gamma = 0.5$ the process very rarely leaves a small region around the equilbirium, while at $\gamma = 0.2$ the process shows periodic behaviour. A similar behaviour is observed in figure 4.4. Comparing this with



$\gamma = 0.34$ $\gamma = 0.32$ $\gamma = 0.3$ $\gamma = 0.28$

$\gamma = 0.26$ $\gamma = 0.24$ $\gamma = 0.22$ $\gamma = 0.2$

FIGURE 4.1: ω-limit sets for the deterministic equation with uptake function $\Phi(N) = \gamma\Phi_T(N) + (1-\gamma)\Phi_I(N)$.

the deterministic results in figures 4.1 and 4.3, we see that the introduction of stochasticity has not produced the kind of qualitative change that it does in, for example, the SIR model with vital dynamics. Therefore, despite the quantitative estimates developed in the earlier sections, we cannot conclude that this form of stochasticity resolves the qualitative issue of hypersensitivity to model structure.

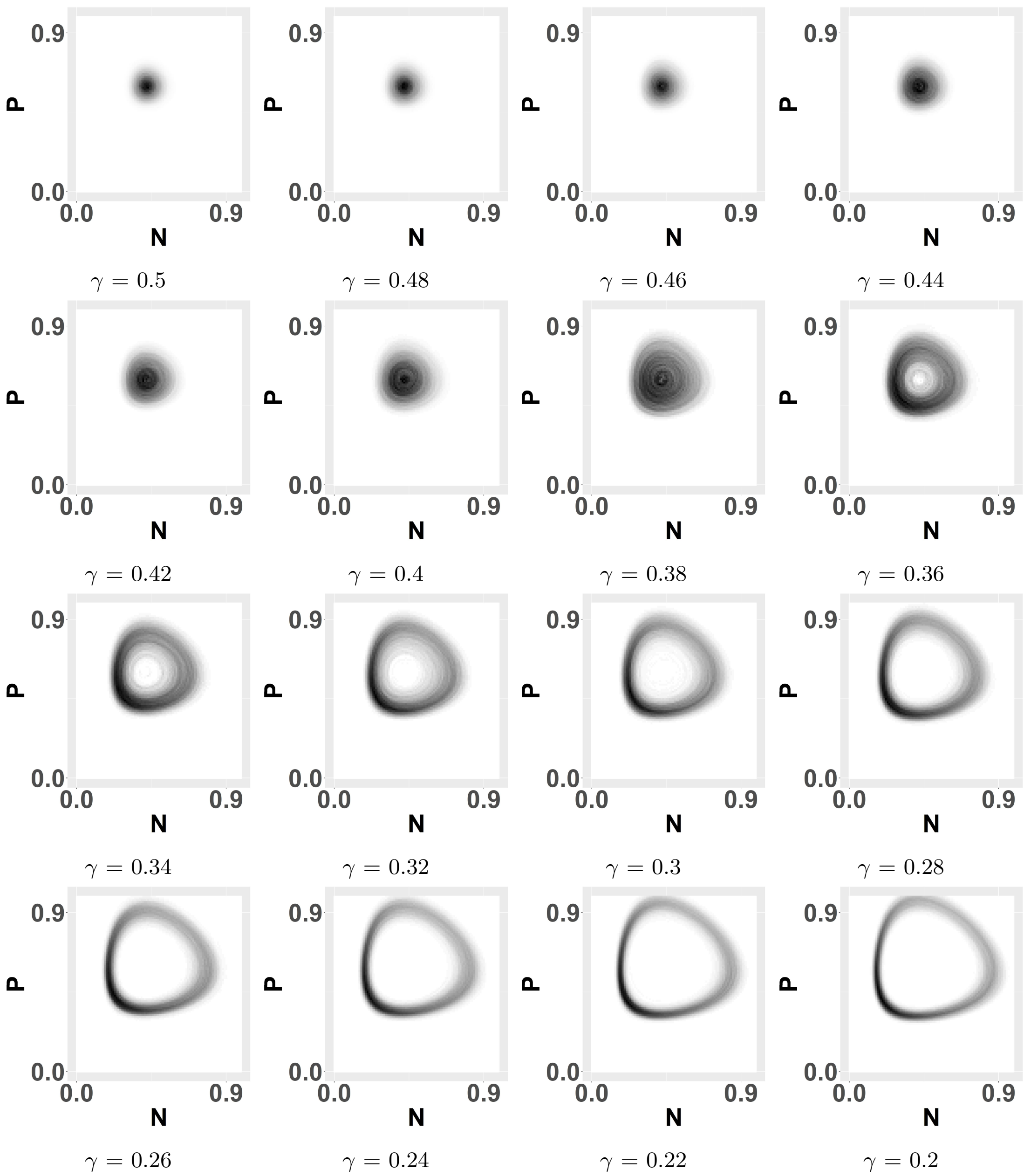


Figure 4.2: Densities of approximate time-invariant probability distributions with jump frequency $c = 12$ and uptake function $\Phi(N) = \gamma\Phi_T(N) + (1-\gamma)\Phi_I(N)$.

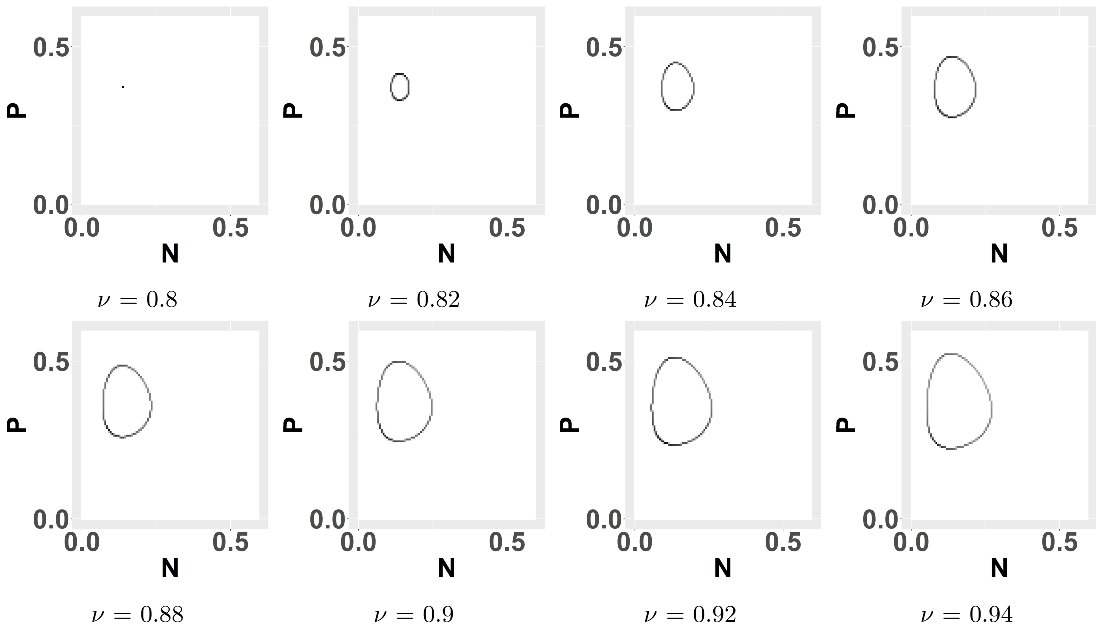


FIGURE 4.3: ω-limit sets for the deterministic equation with uptake function $\Phi(N) = \nu\Phi_H(N) + (1-\nu)\Phi_I(N)$.

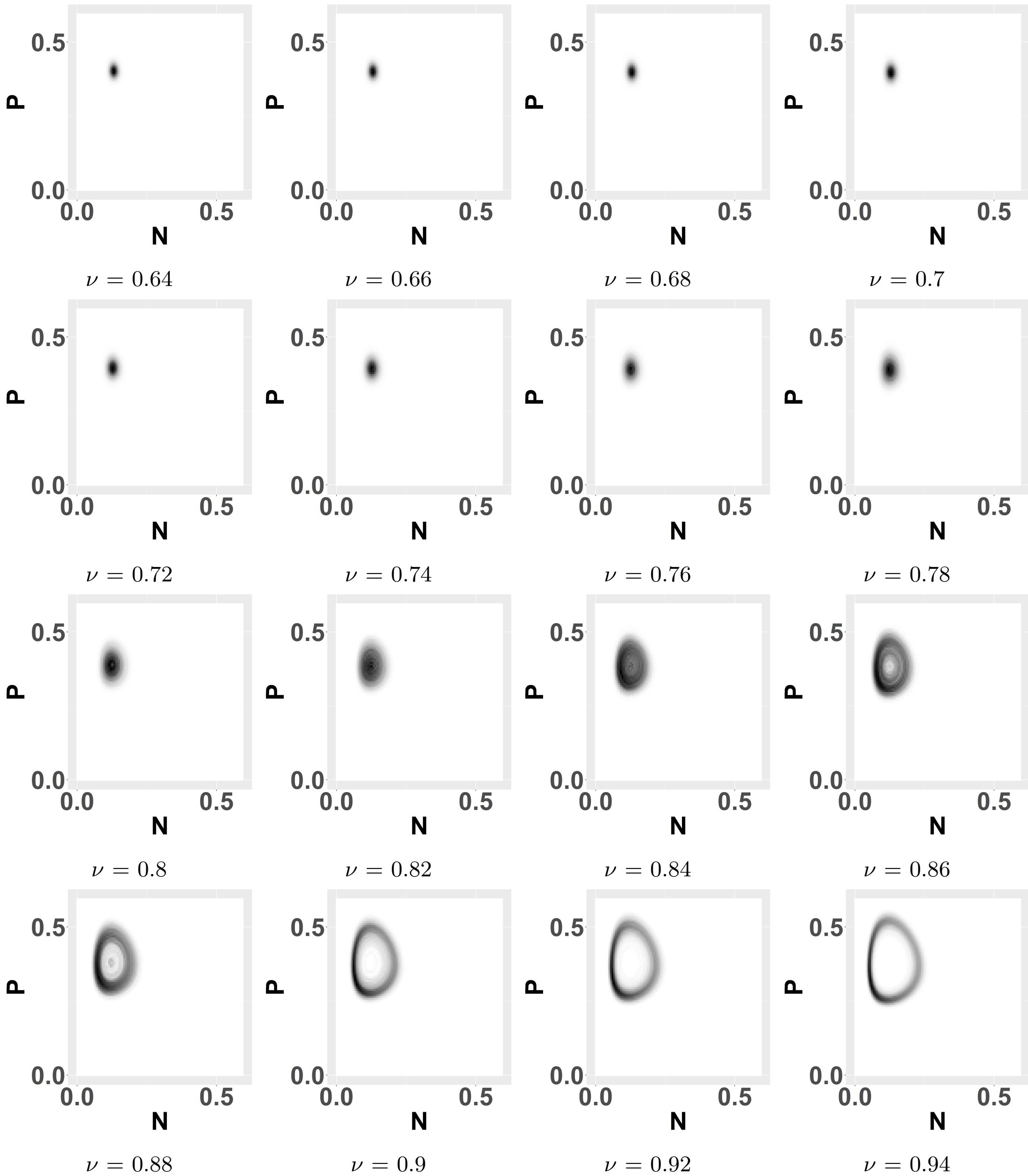


FIGURE 4.4: Densities of approximate time-invariant probability distributions with jump frequency $c = 12$ and uptake function $\Phi(N) = \nu\Phi_H(N) + (1-\nu)\Phi_I(N)$.

Chapter 5

Discussion

Although the introduction of Poisson-driven stochasticity to the ODE model provides a bound on the sensitivity of the steady-state probability distributions to changes in the vector field, the numerical results show that this alone does not resolve the issue of sensitivity to model structure. For example, in figure 4.2 the time-invariant probability distribution is concentrated near a single attracting point when $\gamma = 0.5$, but concentrates near a periodic attractor at $\gamma = 0.2$. This mirrors the transition we see in the deterministic case in figure 4.1, and so the qualitative behaviour differs between the Ivlev and Trigonometric models to a similar degree, both with and without stochasticity. Thus hypersensitivity is present in the Poisson-driven SDE variant of R-M model.

There are many other ways that stochasticity could be incorporated into the R-M model, and a different probabilistic approach could be more successful. One approach is through agent-based models which simulate individual predator and prey agents in a probabilistic framework, as in the paper [8]. Agent-based models circumvent the need for a choice of function ϕ, but the increased complexity of such models still leaves room for the possibility of excessive sensitivity to minor changes in model structure. If such sensitivity is indeed present in agent-based models, this could provide insight into the origins of hypersensitivity in ODE models. This is particularly relevant to the Ivlev and Holling II models, both of which can be derived from scaling limits of agent-based models.

Alternatively, in the article [2] the authors use a probabilistic approach to examine sensitivity to random small perturbations of the uptake function. This work reveals that the different bifurcation behaviours of the Ivlev, Holling II, and trigonometric models are not at all exceptional among possible uptake functions. Instead, they find that a randomly selected perturbation of the uptake function typically has a high chance of changing the stability of the coexistence equilibrium, even if the perturbation is very small in size.

Appendix A

Proof of Proposition 3.1.1

Proof. We begin by proving that any solution to (3.1.2) solves (3.1.1). First observe that for any $v(x,t) \in BL(D \times [0,T])$ we have

$$\partial_t v(X_b(x,t),t) = v_t(X_b(x,t)) + b(X_b(x,t)) \cdot \nabla v(X_b(x,t),t)$$

by the definition of the flow $X_b(x,t)$. Then for any $\mu \in Z$, now assuming $v(x,T) = 0$, we compute

$$\begin{aligned}
&\int_0^T \int_D (\partial_t + b(x) \cdot \nabla - c) v(x,t) d\left(e^{-ct} X^{\#}_{b,t}\mu\right) dt \\
&\quad = \int_0^T \int_D e^{-ct} \left(v_t(X_b(x,t),t) + b(X_b(x,t)) \cdot \nabla v(X_b(x,t),t) - cv(X_b(x,t),t)\right) d\mu dt \\
&\quad = \int_0^T \int_D \partial_t (e^{-ct} v(X_b(x,t),t)) d\mu dt = -\int_D v(x,0) d\mu. \qquad \text{(A0.1)}
\end{aligned}$$

Furthermore, we can use a similar argument to show

$$\begin{aligned}
&\int_0^T \int_0^t \int_D (\partial_t + b(x) \cdot \nabla - c) v(x,t) d\left(e^{-c(t-\tau)} X^{\#}_{t-\tau} A\mu_\tau\right) d\tau dt \\
&\quad = \int_0^T \int_\tau^T \int_D \partial_t (e^{-c(t-\tau)} v(X_b(x,t-\tau),t)) d\left(A\mu_\tau\right) dt d\tau \\
&\quad = -\int_0^T \int_D A^* v(x,\tau) d\mu_\tau d\tau. \qquad \text{(A0.2)}
\end{aligned}$$

Assuming μ_t satisfies (3.1.2), we find that the L.H.S of (3.1.1) can be written as

$$\begin{aligned}
&\int_0^T \int_D (\partial_t + b(x) \cdot \nabla - c) v(x,t) d\left(e^{-ct} X^{\#}_{b,t}\mu_0\right) dt \\
&\quad + \int_0^T \int_0^t \int_D (\partial_t + b(x) \cdot \nabla - c) v(x,t) d\left(e^{-c(t-\tau)} X^{\#}_{t-\tau} A\mu_\tau\right) d\tau dt \\
&\quad + \int_0^T \int_D A^* v(x,t) d\mu_t + \int_D v(x,0) d\mu_0, \qquad \text{(A0.3)}
\end{aligned}$$

which simplifies to 0 by (A0.1) and (A0.2). Next, we prove existence. The equation

(3.1.2) can be solved by a standard iterative procedure. Define a sequence of Z-valued functions $\nu_n(t) : \mathbb{R}^+ \to Z$ by

$$\nu_0(t) = e^{-ct} X^{\#}_{b,t} \mu_0,$$

and

$$\nu_n(t) = \int_0^t e^{-c(t-\tau)} X^{\#}_{t-\tau} A \nu_{n-1}(\tau) d\tau.$$

We prove by induction that these integrals are well-defined in the sense of (1.2.1), and give a bound on their growth. Assume that $\nu_n(t)$ is well-defined for all $t \in \mathbb{R}^+$ and satisfies

$$||\nu_n(t)||_{TV} \leq \frac{t^n ||A||^n_{op(Z,Z)}}{n!}.$$

Then $\forall f \in C^0(D), t \in \mathbb{R}^+$ the function

$$\tau \mapsto \int_D e^{-c(t-\tau)} A^* f(X_b(x, t-\tau)) d\nu_{n-1}(\tau)$$

is continuous for $\tau \in [0, t]$ and hence $\nu_n(t)$ is well-defined for $\forall t \in \mathbb{R}^+$. Additionally, for $f \in C^0(D)$

$$\begin{aligned} \left| \int_D f(x) d\nu_{n+1}(t) \right| &= \left| \int_D \int_0^t e^{-c(t-\tau)} \phi(X_{t-\tau}, \tau) dA\nu_n(\tau) \right| \\ &\leq \int_0^t ||\phi(X_{t-\tau}, \tau)||_{C^0(D)} ||A||_{op(Z,Z)} ||\nu_n(t)||_{TV} \\ &\leq ||f||_{C^0(D)} \frac{t^{n+1} ||A||^{n+1}_{op(Z,Z)}}{(n+1)!}. \end{aligned} \tag{A0.4}$$

Since the base case $\nu_0(t)$ is clearly defined and bounded in TV by 1 the induction argument is complete. It follows that the series

$$\mu_t = \sum_{n=0}^{\infty} \psi_n(t).$$

is uniformly convergent with respect to the total variation norm on any bounded time interval $[0, T]$, and therefore satisfies the integral equation (3.1.2) in the sense of (1.2.1). Note that if $\mu \geq 0$ then $A\mu \geq 0$ and also

$$||A\mu||_{TV} = \int_D \int_D \sigma(x, y) d\mu(x) dy = ||\mu||_{TV}.$$

It follows then that if $\mu_0 \geq 0$ then $\mu_t \geq 0$ for all t, and from (3.1.2) we see that

$$||\mu_0||_{TV} = ||\mu_t||_{TV}, \ \forall t \in \mathbb{R}^+.$$

Applying the Hahn-Jordan decomposition to μ_0, (3.1.3) and (3.1.4) follow by linearity.

Finally, we prove the uniqueness of μ_t. It suffices to prove that $\mu_0 = 0$ implies that $\mu_t = 0$ for all $t \in \mathbb{R}^+$. We achieve this by constructing a solution $v(x,t) \in C^1(D \times [0,T])$ to

$$(\partial_t - b(x) \cdot \nabla - (cA^* - c))v(x,t) = p(x,t), \qquad x, t \in D \times [0,T], \; v(x,0) = 0. \tag{A0.5}$$

for an arbitrary $p(x,t) \in C^1(D \times [0,T])$. Then using $v(x, T-t)$ as a test function in (3.1.1), we obtain

$$\int_0^T \int_D p(x, T-t) d\mu_t = 0$$

$\forall p(x,t) \in C^1(D \times [0,T])$ if $\mu_0 = 0$, which suffices to conclude that $\mu_t = 0$, since C^1 is dense in C^0.

To construct $v(x,t)$, we assume it is a solution of

$$v(x,t) = \int_0^t [cA^*v](X_b(x,t-\tau),\tau) - cv(X_b(x,t-\tau),\tau) + p(X_b(x,t-\tau),t-\tau)d\tau. \tag{A0.6}$$

Once again we can construct a solution of this equation by an iterative process. We will not repeat the argument here since it is standard.

To show that $v(x,t)$ satisfying (A0.6) solves (A0.5), assume that $y \in D$ is such that $X(y,-t)$ is well-defined. Substituting $X(y,-t)$ into (A0.6) gives

$$v(X(y,-t),t) = \int_0^t [cA^*v](X(y,-\tau),\tau) - cv(X(y,-\tau),\tau) + p(X(y,-\tau),\tau)d\tau, \tag{A0.7}$$

and differentiating this entire expression with respect to t we obtain

$$v_t(X(y,-t),t) - b(X(y,-t)) \cdot \nabla v(X(y,-t),t) = [cA^*v](X(y,-t),t) - cv(X(y,-t),t) + p(X(y,-t),t). \tag{A0.8}$$

For every $x \in D$ and $t \in \mathbb{R}^+$, there is some $y \in D$ such that $x = X(y,-t)$. This implies that $v(x,t)$ solves (A0.5) for each $(x,t) \in D \times [0,T]$. Since any solution of (3.1.2) solves (3.1.1), and the solution of (3.1.1) is unique, it follows that the solution of (3.1.2) that we constructed is the unique solution of both formulations, completing the only if.

The semigroup property follows easily from the uniqueness of the solution. □

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