FUZZY DIFFERENTIAL INCLUSIONS AS SUBSTITUTES FOR STOCHASTIC DIFFERENTIAL EQUATIONS IN POPULATION BIOLOGY

PETER ANTONELLI[1]

Department of Mathematics, University of Alberta, Edmonton, Canada T6G 2G1

VLASTIMIL KŘIVAN[2]

Biological Research Center, Branišovská 31, 370 05 České Budějovice, Czechoslovakia

Abstract. The familiar procedure of adding whitenoise to deterministic systems of equations may not be appropriate, or even possible in some modelling problems arising in the biological sciences. Although some mathematical handle on indeterminant factors (i.e. "noise") may be necessary, sometimes the probabilistic requirements involved can not be rigorously verified for the data set in hand. As an alternative, we discuss here the modelling utility of fuzzy differential inclusions associated with given systems of nonlinear ode's. We give concrete examples and give account of the conservative stochastic mechanics of E. Nelson applied to growth of a dimorphic clone, and its fuzzy differential inclusion analogue.

1. INTRODUCTION

In certain problems occuring in physiology, ecology and biophysics and other fields it may be impossible to use stochastic differential equations to model noise, for not infrequently, the statistical prerequisites are not known to hold with certainty nor are the fundamental assumptions of Markov diffusions. In fact, in some areas the addition of noise seems to present almost insurmountable problems. For example, a system arrising in modelling growth of a colonial clone in a noisy environment is

$$dx^i(t) = N^i(t)dt + e^{-\phi(x(t))}dw^i(t), \quad i = 1, \ldots, n \tag{1}$$

$$dN^i(t) = H^i(x(t), N(t))dt + d\eta^i(t), \quad i = 1, \ldots, n \tag{2}$$

where $e^{-\phi(x)}$ is a positive variance and in many applications $\phi(x) = \sum_{i=1}^n \alpha_i x^i$ with $\alpha_i > 0, i = 1, \ldots, n$. This system of equations models the concept of *developmental noise* due to the great embryologist C.H. Waddington, [21], for a polymorphic clone of n morphotypes, in which the x^i is biomass measuring the accumulation produced by the i-th type of production module, whose number is N^i. Thus, there are $2n$ variables $x^1, \ldots, x^n, N^1, \ldots, N^n$ and a given C^r-function $\phi(x^1, \ldots, x^n)$ as well as Brownian motions $w^i(t)$ and $\eta^j(t)$ which may be independent or not. Futher, Lotka-Volterra type interactions, typical of coral clones, lead us to consider

$$H^i(x, N) = -\sum_{j,k=1}^n \Gamma^i_{jk}(x, N)N^j N^k + \lambda_i N^i \tag{3}$$

[1]Partially supported by NSERC A-7667
[2]Partially supported by NSERC A-7667, Univesity of Alberta Research Fund and CAS 18002

where $\Gamma^i_{jk}(x,N)$ are n^3 functions, typically constants, and λ_i are n growth rates, see [1]. For evolutionary coexistence of different morphotypes in an individual clone it is necessary to have all $\lambda_i = \lambda$, $i = 1, \ldots, n$. Neglecting noise terms in (1), (2) we obtain

$$\frac{d^2x^i(t)}{dt^2} + \sum_{j,k=1}^{n} \Gamma^i_{jk} \frac{dx^j(t)}{dt} \frac{dx^k(t)}{dt} - \lambda \frac{dx^i(t)}{dt} = 0, \quad i = 1, \ldots, n \tag{4}$$

which are Euler-Lagrange equations for the problem of optimization with disccounting function $e^{-\lambda t}$, in the calculus of variations for the following functional

$$\int_{t_o}^{t_1} e^{2\phi(x)} \sum_{i=1}^{n} (N^i)^2 e^{-\lambda t} dt, \tag{5}$$

with some fixed endpoints $x(t_0) = x_0$, $x(t_1) = x_1$. In fact, it is a far from trivial theorem that $\phi(x) = \sum_{i=1}^{n} \alpha_i x_i$ is the only possible function which yields non-trivial constant Γ^i_{jk}, see [1], p. 151-157. Moreover,

$$\begin{aligned}
\Gamma^i_{ii} &= \frac{\partial\phi(x)}{\partial x^i} = \alpha_i \\
\Gamma^i_{ij} = \Gamma^i_{ji} &= \frac{\partial\phi(x)}{\partial x^j} = \alpha_j, \quad i \neq j \\
\Gamma^i_{jj} &= -\frac{\partial\phi(x)}{\partial x^i} = -\alpha_i, \qquad i \neq j \\
\Gamma^i_{jk} &= 0, \qquad\qquad\qquad\quad i \neq j \neq k.
\end{aligned}$$

The solutions of equations (4) are actually geodesics when reparametrized by total size $s(t) = A + Be^{+\lambda t}$ of the clone, in a Riemannian geometry whose arc length functional is defined

$$ds^2 = e^{2\phi(x)} \sum_{i=1}^{n} (dx^i)^2,$$

see [(26), with y^i replaced by x^i and $a = 0$] for two dimensional case. This particular parametrization of size makes sense for the "open growth" of community ecology where no "adult size" exists as it does for growth of individual organisms, as in section 4. See ([17], p.110) for introduction to Riemannian geometry. For the general Riemannian space the arc length is given by the tensor $g_{ij}(x)$ according

$$ds^2 = \sum_{i,j=1}^{n} g_{ij}(x) dx^i dx^j, \tag{6}$$

while $g_{ij}(x)$ has inverse decomposed locally into

$$g^{ij}(x) = \sum_{k=1}^{n} \sigma^i_k(x) \sigma^j_k(x)$$

and (1), (2) are written

$$dx^i(t) = N^i(t)dt + \sum_{k=1}^{n} \sigma^i_k(x) dw^k(t) \tag{7}$$

$$dN^i(t) = H^i\big(x(t), N(t)\big)dt + d\eta^i(t). \tag{8}$$

System of the form (7), (8) with $H^i(x,N)$ defined by (3), have been used to model integrated communities of n coral species, [1], as well as a host-parasite system [6], [7] and a model of toxic interactions between soft and hard corals, where Γ^i_{jk} depend on x^i, [2], [5]. Indeed, (7), (8) model the coral-signal in the nonlinear filtering problem based on a starfish-predator equation with noise as observation process, [8]. Whereas the field data on starfish support the conclusion of the underlying deterministic equations [13] the addition of noises as above have not been rigorously verified. However, parameter estimations can be performed for the separate species in the laboratory. Yet, the question of whether or not the data accurately describe a Markov process is far from answered. Therefore in this case (7), (8) may not in the long run be appropriate and a simpler substitute may be a better representation.

However, in the case of ecological modelling highly social interactions à la G.E. Hutchinson (i.e. higher order density-dependent coefficients all which scale quadratically [9]), the deterministic system representing growth must permit Γ^i_{jk} to depend explicitly on N^i/N^j, see example (22) below. The resulting geometry on the production space $x^1, \ldots, x^n$ variables is defined by a zero degree (positively) homogeneous in N^i, metric tensor, $g_{ij}(x, N)$. This is precisely the realm of Finsler differential geometry and the presence of N^i in g^{ij} is exactly the obstruction to the existence of a Markov diffusion on production space. The infinitesimal generator G of the formal equation

$$dx^i(t) = N^i(t)dt + \sum_{k=1}^{n} \sigma^i_k(x(t), N(t))dw^k(t) \tag{9}$$

would seem to be

$$G = 1/2\Delta_g + \sum_{i=1}^{n} N^i \frac{\partial}{\partial x^i} \ ,$$

where

$$\Delta_g = \sum_{i,j=1}^{n} g^{ij}(x, N)(\frac{\partial^2}{\partial x^i \partial x^j} - \sum_{k=1}^{n} \Gamma^k_{ij}(x, N) \frac{\partial}{\partial x^k})$$

is the apparently appropriate Laplacian. (It would be of this form for Riemannian geometry.) But, it is obvious that Δ_g *does not* define a Markov diffusion on production space for the Finsler case because $g^{ij}(x, N)$ depends on N^i. In fact, the formal equation (9) should be understood as integral equation

$$x^i(t) = x^i(t_0) + \int_{t_0}^{t} N^i(\tau)d\tau + \int_{t_0}^{t} \sum_{k=1}^{n} \sigma^i_k(x, N)dw^k, \tag{10}$$

where the second integral is Itô stochastic integral. But this integral is defined only when σ^i_k doesn't depend on N, the mean forward velocity, see [15]. Thus, formal equation (9) has meaning only when σ^i_k is independent of N. Efforts of the first author to construct an appropriate Brownian motion theory for (10) on the tangent bundle has several difficulties and remains too complicated for practical use, thus far.

2. FUZZY DIFFERENTIAL INCLUSIONS

In this part we reformulate stochastic differential equations (8), (9) as a fuzzy differential inclusion, thus allowing σ^i_k depend not only on x but also on N. This reformulation has two advantages:

1) *The corresponding fuzzy differential inclusion is well defined (with contrast to (9)) and has a solution.*

2) *Using fuzzy differential inclusions allows us to define "likelihood" and thus develop a non-stochastic analog of systems with uncertain dynamics.*

The concept of fuzzy differential inclusions generalizes the notion of differential inclusion. They were introduced in [11] and in slightly different form they were used to define "likelihood" for a solution to a differential inclusion in a nonprobabilistic framework in [14].

One of the main differences between stochastic differential equations and fuzzy differential inclusions is that while solutions to the first are nowhere differentiable functions the solutions for the second are absolutely continuous functions and consequently they are differentiable almost everywhere.

To reformulate (8), (9) as a fuzzy differential inclusion we will take underlying deterministic system and add "noise" into the right hand side, i.e.

$$\dot{x}^i(t) = N^i(t) + \sum_{k=1}^{n} \sigma_k^i(x(t), N(t))w^k(t) \tag{11}$$

$$\dot{N}^i(t) = H^i\big(x(t), N(t)\big) + \eta^i(t). \tag{12}$$

Here we asssume that the bounds for the "noises" are known, i.e.

$$\begin{aligned} w^k(t) \in [a^k, b^k], \quad a^k < b^k \quad \text{for all} \quad k = 1, \dots n, \\ \eta^i(t) \in [c^i, d^i], \quad c^i < d^i \quad \text{for all} \quad i = 1, \dots, n. \end{aligned}$$

It is assumed that the functions $w(t)$ and $\eta(t)$ are measurable. We do not assume anything about statistical properties of the "noises." System (11), (12) may be rewritten as a differential inclusion, (for more information on differential inclusions we refer to [12]),

$$\begin{cases} \dot{x}^i(t) & \in N^i(t) + [\sum_{k=1}^n \sigma_k^i(x(t), N(t))a^k, \sum_{k=1}^n \sigma_k^i(x(t), N(t))b^k] \\ \\ \dot{N}^i(t) & \in H^i\big(x(t), N(t)\big) + [c^i, d^i]. \end{cases} \tag{13}$$

Any absolutely continuous functions $x^i(t), N^i(t),\ i = 1, \dots, n$ satisfying (13) almost everywhere with respect to Lebesque measure are *solutions* to (13). The system (13) may be considered as a non-stochastic counterpart of (8), (9) when the noise does not need the "microscopic" sample path structure of white noise. In fact, when σ_k^i and H^i are assumed to be continuous, Corollary 7, of [12] implies, for any solution (13) there exist measurable $w^k(t)$ and $\eta^i(t)$ such that (11) and (12) are satisfied. The following proposition follows directly from existence theorem for differential inclusions, see [12].

Proposition 1. *Let $H^i : \boldsymbol{R}^n \times \boldsymbol{R}^n \mapsto \boldsymbol{R}^n$, $\sigma_k^i : \boldsymbol{R}^n \times \boldsymbol{R}^n \mapsto \boldsymbol{R}$, $i = 1, \dots, n$, $k = 1, \dots, n$ be continuous functions then differential inclusion (13) has a solution.*

As stated, (13) doesn't make any assumptions concerning "distribution" of the noise. We may use fuzzy formulation of (13) that allows us to include the information on "distribution" of the noise. We recall here some basic facts on fuzzy differential inclusions and fuzzy likelihood, see [14]. Let X denote a finite dimensional Euklidian space.

Definition 1. Any extended function $U : X \to [0, 1] \cup \{-\infty\}$ is called a membership function of a fuzzy set, or a fuzzy set. We say that the fuzzy set $U(\cdot)$ is closed if its membership function is upper semicontinuous, and non-trivial if it is not identically $-\infty$.

Every fuzzy set is described through its membership function that says "how much" a point belongs to the fuzzy set. If $U(x) = -\infty$ it means that the point x doesn't belong to the fuzzy set at all.

Let us recall the definition of fuzzy set-valued map.

Definition 2. Let $K \subset X$. Any single-valued map $\mathcal{F} : K \times X \to [0, 1] \cup \{-\infty\}$ is called a fuzzy set-valued map, with the fuzzy sets $\mathcal{F}(x, \cdot)$ as values. A fuzzy set-valued map $\mathcal{F}$ is said to be closed if it is upper semicontinuous, and with convex values if, for every $x \in K$, $\mathcal{F}(x, \cdot)$ is concave; $\mathcal{F}$ is locally bounded if there exists $M > 1$ and $T > 0$ such that

$$\|x\| \le MT \Longrightarrow \sup\{\|v\| \,|\mathcal{F}(x, v) > -\infty\} \le M \ .$$

The domain of $\mathcal{F}$ is the set $\{(x,v) \mid \mathcal{F}(x,v) > -\infty\}$.

Let $y = (x,N) \in \boldsymbol{R}^{2n}$ and let us denote the right hand side of (13) by $F(y)$. Then (13) is the following differential inclusion

$$\dot{y}(t) \in F\big(y(t)\big). \tag{14}$$

Let us consider the right hand side of (14) as a fuzzy set-valued map described through $\mathcal{F}(y,z)$. Let

$$\mathcal{F}(y,z) = \begin{cases} \xi \in [0,1] & \text{if} \quad z \in F(y) \\ -\infty & \text{if} \quad z \notin F(y). \end{cases} \tag{15}$$

Then solutions to (14) are solutions to the following fuzzy differential inclusion

$$\mathcal{F}(y(t), \dot{y}(t)) > -\infty.$$

Let $S(y_0)$ be the set of all solutions to (14) with initial condition $y(0) = y_0$. Then for any solution $y(t) \in S(y_0)$ we may define its "likelihood" $\mathcal{L}(y)$,

$$\mathcal{L}(y) := 1/T \int_0^T \mathcal{F}(y(t), y'(t))dt. \tag{16}$$

The following theorem follows from existence theorem for upper semicontinuous differential inclusions and Tonelli theorem, (see [14]).

Proposition 2. *Let $K := B[0,TM]$. Let $\mathcal{F}$ be a closed, locally bounded fuzzy set-valued map with non-trivial convex values. Then the set $S(y_0)$ is non-empty and compact, and the map $\mathcal{L} : S(y_0) \to [0,1] \cup \{-\infty\}$ is upper semicontinuous.*

From this proposition follows that *there exists a solution for the fuzzy differential inclusion that maximizes $\mathcal{L}$.*

The main question is which fuzzy function $\mathcal{F}$ one should choose. In "soft sciences" the typical situation is that we do not know anything about the noise but boundedness. However, common sense leads to the conclusion that the points on the boundary of the set $F(y)$ are not "likely," while points in the interior are more "likely". This lead in [14] to propose the following fuzzy function as a general candidate to model noise.

Denote by $b(y)$ the barycenter of $F(y) + B$ (see [12]), i.e.

$$b(y) := \frac{1}{m_n(F(y)+B)} \int_{F(y)+B} z dm_n,$$

which is well defined because $F(y) + B$ has positive measure in $X = \boldsymbol{R}^n$. Here m_n stands for $n-$dimensional Lebesque measure. Moreover, $b(x) \in ri\ F(x)$ and, by Theorem 1, p.77 in [12], $b(\cdot)$ is a continuous selection from a continuous set-valued map $F(\cdot)$. If additionally $F(\cdot)$ is Lipschitzean then $b(\cdot)$ is also Lipschitzean.

Definition 3. Let $F : X \to 2^X$ be a set-valued map. We define for it the fuzzy set-valued map $\mathcal{F}$ as

$$\mathcal{F}(x,y) := \begin{cases} \sup\{z \in \boldsymbol{R} \mid (y,z) \in \text{ conv}\{(F(x) \times \{0\}) \cup \{(b(x),1)\}\}\} & \text{if} \quad y \in F(x) \\ -\infty & \text{otherwise.} \end{cases}$$

The meaning of this fuzzy function is to give maximum likelihood to the barycenter of $F(y)$, while the points on the boundary of $F(y)$ have likelihood equal to zero, see [14].

Proposition 3. *For (13), $\mathcal{F}(x,N,\dot{x},\dot{N})$ has the following form*

$$\mathcal{F}(x,N,\dot{x},\dot{N}) = 1 - \max\{\max_{i=1,\dots,n} \frac{|2(\dot{N}^i - H^i(N)) - c^i - d^i|}{c^i + d^i},$$

$$\max_{i=1,\dots,n} \frac{|2(\dot{x}^i - N^i) - \sum_{k=1}^n \sigma_k^i(x,N)a^k - \sum_{k=1}^n \sigma_k^i(x,N)b^k|}{\sum_{k=1}^n \sigma_k^i(x,N)a^k + \sum_{k=1}^n \sigma_k^i(x,N)b^k}\}$$

if $(\dot{x},\dot{N}) \in F(x,N)$ *and* $\mathcal{F}(x,N,\dot{x},\dot{N}) = -\infty$ *if* $(\dot{x},\dot{N}) \notin F(x,N)$.

If we assume that set-valued map $F(\cdot)$ is Lipschitz, it follows from [14] that the trajectory $y(t)$ that maximizes fuzzy likelihood satisfies the following differential equation for the barycenter

$$\dot{y}(t) = b(y(t)), \quad \text{on} \quad [0,T] \tag{17}$$

is unique. Equation (17) gives the deterministic system

$$\begin{aligned} \dot{x}^i(t) &= N^i(t) \\ \dot{N}^i(t) &= H^i\big(x(t),N(t)\big). \end{aligned}$$

3. AN EXAMPLE OF NON-RIEMANNIAN TYPE

Various generalizations of (1), (2) are possible from considering generalizations of the Lagrangian (5). For example, the variation

$$\delta \int_{t_0}^{t_1} e^{2\phi(x)} \big[\sum_{i=1}^{2} (N^i)^m\big]^{2/m} e^{-\lambda t} dt = 0 \tag{18}$$

where $m \geq 3$, leads to *Finsler variational problems* in which the Riemannian metric tensor $g_{ij}(x)$ is replaced by

$$g_{ij}(x,N) := \frac{1}{2}\frac{\partial^2 L(x,N)}{\partial N^i \partial N^j}$$

with

$$L(x,N) := e^{2\phi(x)} \big[\sum_{i=1}^{2} (N^i)^m\big]^{2/m}. \tag{19}$$

A stochastic differential equation analogue of the Riemannian case, $m = 2$, requires use of the square root $\sigma_k^i(x,N)$ of $g^{ij}(x,N) = (g_{ij}(x,N))^{-1}$. Since $g^{ij}(x,N)$ is positive definite and differentiable on the set of (x,N) where $N \neq 0$, $\sigma_k^i(x,N)$ exists and will be differentiable with Hölder conditions on specific order partial derivatives, if $g_{ij}(x,N)$ has these properties (eg. if $g^{ij}(x,N)$ is C^∞, then $\sigma_k^i(x,N)$ is Lipschitz) see [15].

Since we have $g_{ij}(x,N) = e^{2\phi(x)}\tilde{g}_{ij}(N)$ with

$$\left.\begin{aligned} \tilde{g}_{11}(N) &= \frac{(N^1)^{m-2}[(N^1)^m + (m-1)(N^2)^m]}{[(N^1)^m + (N^2)^m]^{2-\frac{2}{m}}} \\ \tilde{g}_{22}(N) &= \frac{(N^2)^{m-2}[(N^2)^m + (m-1)(N^1)^m]}{[(N^1)^m + (N^2)^m]^{2-\frac{2}{m}}} \\ \tilde{g}_{12}(N) = \tilde{g}_{21} &= \frac{(2-m)(N^1N^2)^{m-1}}{[(N^1)^m + (N^2)^m]^{2-\frac{2}{m}}} \\ \text{and} \quad \det(\tilde{g}_{ij}(N)) &= \frac{(m-1)(N^1N^2)^{m-2}}{[(N^1)^m + (N^2)^m]^{\frac{2m-4}{m}}} \end{aligned}\right\} \tag{20}$$

(see [20], p. 17), we can write for its inverse

$$
\left.\begin{aligned}
g^{ij}(x,N) &= \sum_{k=1}^{2} \sigma_k^i(x,N)\sigma_k^j(x,N)\\
\text{where}\quad \sigma_k^i(x,N) &= e^{-\phi(x)}\tilde{\sigma}_k^i(N)\\
\text{and}\quad \tilde{g}^{ij}(N) &= \sum_{k=1}^{2} \tilde{\sigma}_k^i(N)\tilde{\sigma}_k^j(N).
\end{aligned}\right\} \tag{21}
$$

Consider now the 2^{nd} order system [4], [9]

$$
\begin{aligned}
\frac{dN^1}{dt} &= \lambda N^1 - \alpha_1(N^1)^2 - \delta_1 N^1N^2 + (\delta_2-\alpha_1)\Big(\frac{N^2}{N^1}\Big)^{m-2}(N^2)^2\\
\frac{dN^2}{dt} &= \lambda N^2 - \alpha_2(N^2)^2 - \delta_2 N^1N^2 + (\delta_1-\alpha_2)\Big(\frac{N^1}{N^2}\Big)^{m-2}(N^1)^2.
\end{aligned} \tag{22}
$$

Here, α_i, δ_i are positive constants, $i=1,2$, as is λ and $m \geq 2$ is a fixed positive integer.

Theorem (Antonelli and Lin). *The system (22) exhibits a positive steady-state at*

$$
\left.\begin{aligned}
N_0^1 &= \frac{\lambda(\delta_2-\alpha_1)^{\frac{1}{m-1}}}{\alpha_1(\delta_2-\alpha_1)^{\frac{1}{m-1}} + \alpha_2(\delta_1-\alpha_2)^{\frac{1}{m-1}}}\\
N_0^2 &= \Big(\frac{\delta_1-\alpha_2}{\delta_2-\alpha_1}\Big)^{\frac{1}{m-1}} N_0^1.
\end{aligned}\right\} \tag{23}
$$

Moreover, this steady-state is unique and globally asymptotically stable for the set $\boldsymbol{R}_+^2$.

If we augment (22) with production equations $dx^i = N^i dt$ $(i=1,2)$ then we can prove the

Theorem. *The production equations defined by (22) are extremals of the Lagrangian (19) with* $\phi = \sum_{i=1}^{2} \alpha_i x^i$, *if and only if* $\delta_1 = \frac{m\alpha_2}{m-1}$ *and* $\delta_2 = \frac{m\alpha_1}{m-1}$. *If* $m=2$, *then, as proved in [1, p. 151-157], the homogeneous Lagrangian (19) is the only one which can produce constant coefficients* Γ_{jk}^i.

The $(m=2)$ case does have a meaningful stochastic analogue in (1),(2) above. Although we do not know the stochastic analogue of (1),(2) for $m \geq 3$, as explained above, we are able to write the differential inclusion analogue (13). Namely,

$$
\begin{aligned}
\dot{x}^i(t) &\in N^i(t) + \Big[\sum_{k=1}^{2} \sigma_k^i\big(x(t),N(t)\big)a^k,\ \sum_{k=1}^{2} \sigma_k^i\big(x(t),N(t)\big)b^k\Big]\\
\dot{N}^i(t) &\in \lambda_i N^i - \sum_{j,k}^{2} \Gamma_{jk}^i\big(N(t)\big)N^jN^k + [c^i, d^i]
\end{aligned} \tag{24}
$$

where, $\Gamma_{jk}^i(N)$ are given by

$$
\Gamma_{11}^1(N) = \alpha_1 - \frac{\alpha_1}{2}(m-2)\Big(\frac{N^2}{N^1}\Big)^m; \quad \Gamma_{12}^1(N) = \frac{m}{2(m-1)}\ \Big[\alpha_2 + (m-2)\alpha_1\Big(\frac{N^2}{N^1}\Big)^{m-1}\Big]
$$

$$
\Gamma_{22}^1(N) = -\ \frac{m}{2}\ \alpha_1\Big(\frac{N^2}{N^1}\Big)^{m-2}
$$

with $\Gamma^2_{22}(N), \Gamma^2_{21}(N), \Gamma^2_{11}(N)$ given by interchanging indices 1 and 2 in these three formulas ($\Gamma^i_{jk}(N) = \Gamma^i_{kj}(N)$) (see [4], [10]).

The solution with maximal likelihood for fuzzy version of (24) satisfies the equation for barycenter (17) and consequently (22) with $dx^i = N^i dt$. Since in the set $\boldsymbol{R}^4_+ \cap \{x_i \geq \epsilon,\ N_i \geq \epsilon,\ i = 1, 2\}$, $\epsilon > 0$, the right hand side of (24) is Lipschitzian, (17) has unique solution. Note that global asymptotic stability of (N^1_0, N^2_0) insures that *myopic* optimality extends to long-time optimality for this autonomous system.

4. TARGETING GROWTH IN THE PRESENCE OF NOISE

We now make use of Nelson's famous conservative diffusion theory, [19], to model the canalization of developmental growth, [21]. This theory of Nelson's was motivated by problems in Quantum Mechanics, but as long ago as 1980, it was pointed out by, Nagasawa, that it has use in biology, as well, [18].

There has been extensive study of organ growth in animals which prove that the final adult forms of most vertebrates are tightly *canalized* about their means, statistically speaking. Both the distribution of *production rates* and the *total biomasses* in all the "phenotypic dimensions" have small variances as time approaches the time of full maturation, [3]. The classic experimental work of the Nobel physiologist, Sir Peter Medawar, on young chicken heart tissue shows this "targeted" property for adult biomass, quite well. In fact, Medawar shows that growth of chick heart tissue ($\sim$ 18 days old) is well-described by a Gompertz growth curve, by sound statistical procedures, [3]. Does addition of noise to Gompertz dynamics yield targeted biomass?

The main reference here is [13]. The system

$$\begin{aligned} dy(t) &= N(t)dt \\ dN(t) &= -\lambda N(t)dt + \nu d\omega(t) \end{aligned} \tag{25}$$

has Gompertz curve solutions if $\nu = 0$ and $y_0 > 0, N_0 > 0$ for initial conditions. Yet, with positive variance, ν^2, (25) exhibits a *divergent* variance for y as time increases, and a finite variance for N, [13]. If, $-\beta\ y\ dt$, ($\beta > 0$), is added to the right-hand side of the second equation of (25), the problem remains. To rectify this problem the 2$^{\text{nd}}$ order form of the equations (25) with $\nu = 0$ suggests use of Nelson's stochastic mechanics.

The Nelson stochastic mechanics provides a model of C.H. Waddington's *developmental noise,* based on a generalization of Medawar's concept of *Growth Energy,* which was used by him to *measure* the growth of chicken embryonic heart tissue, as discussed in [3]. *This Nelson theory will yield targeted biomass as well as targeted population sizes of the castes or morphotypes in homeostosis* (i.e. adult size equilibrium maintenance levels of production).

We now give a detailed example of a dimorphic clone (i.e. dimension 2) in a constant non-zero environment (constant temperature, etc.) whose Nelson mechanics exhibits targeted biomass for the adult or homeostatic form.

Consider the deterministic system (4)

$$\begin{aligned} -a\alpha_1 &= \frac{d^2y^1}{ds^2} + 2\alpha_2 \frac{dy^1}{ds}\frac{dy^2}{ds} + \alpha_1\Big[\Big(\frac{dy^1}{ds}\Big)^2 - \Big(\frac{dy^2}{ds}\Big)^2\Big] \\ -a\alpha_2 &= \frac{d^2y^2}{ds^2} + 2\alpha_1 \frac{dy^1}{ds}\frac{dy^2}{ds} + \alpha_2\Big[\Big(\frac{dy^2}{ds}\Big)^2 - \Big(\frac{dy^1}{ds}\Big)^2\Big] \end{aligned} \tag{26}$$

where $s(t) = A - \frac{\sqrt{\alpha_1^2+\alpha_2^2}}{\lambda}\, e^{-\lambda t}$ has been used as path parameter for targeted growth and external constant force in the environment has been added to the left hand side. Here we have introduced constant $a > 0$ on the right hand side of (26) for later convenience. Let us define on $\boldsymbol{R}^2$

$$V(y) = \frac{a}{2}\, e^{2\phi(y)}, \quad \phi(y) = \alpha_1 y^1 + \alpha_2 y^2,$$

then $g^{ij}(y) = (g_{ij}(y))^{-1}$ is used to define the gradient of $V(y)$ as

$$a\alpha^i = \text{grad}_g^i V(y) := \sum_{j=1}^{2} g^{ij}(y)\, \frac{\partial V(y)}{\partial y^j}, \quad i = 1, 2.$$

Theorem. *The scaler curvature R of the Riemannian geometry, g_{ij}, vanishes identically, and so there is a coordinate transformation to polar coordinate r, θ. It is defined by*

$$r(y^1, y^2) = e^{\phi}(y^1, y^2), \quad \theta(y^1, y^2) = \alpha_2 y^1 - \alpha_1 y^2,$$

so that (26) becomes

$$\left.\begin{aligned} \frac{d^2 r(s)}{ds^2} - r\, \Big(\frac{d\theta(s)}{ds}\Big)^2 &= -kr(s) \\ \frac{d^2\theta(s)}{ds^2} + \frac{2}{r}(s)\, \frac{dr(s)}{ds}\, \frac{d\theta(s)}{ds} &= 0 \end{aligned}\right\} \tag{27}$$

where $k = a(\alpha_1^2 + \alpha_2^2)$ and $s(t) = A - Be^{-\lambda t}$, are convenient definitions of constants and the path parameter, s. Vanishing of R is a necessary and sufficient condition for existence of a coordinate transformation taking 2-dimensional Riemannian geodesics to cartesian (or polar) straight line equations as in (27). (See [17]).

Of course, (26) are just the Euler-Lagrange equations for the Lagrangian

$$L(y) = \frac{1}{2}\, e^{2\phi(y)} \Big(\big(\frac{dy^1}{ds}\big)^2 + \big(\frac{dy^2}{ds}\big)^2 \Big) - V(y).$$

Nelson's Theory of stochastic variational calculus will allow such a classical Lagrangian to play a stochastic role yet still be very close to classical theory.

Let us proceed generally at first, so fix a time interval $[0, S]$, initial density $\rho_0(y)$ and drift vector $b_0(y)$ and consider inhomogeneous Markov diffusions $\xi(s)$ with defining infinitesimal generator

$$\frac{\nu^2}{2}\, \Delta_g + \langle b(y,s), \text{grad}_g \rangle \quad (\Delta_g \quad \text{is the Riemannian Laplacian})$$

where $b(y, 0) = b_0(y)$ and ξ_0 is the initial random 2-dimensional vector with density $\rho_0(y)$. For this class of diffusions the expectation

$$\mathbb{E}\{\int_0^S [\tfrac{1}{2} \sum_{i,j=1}^{n} g_{ij}\xi^i(s)\xi^j(s) - V(\xi(s))]ds\} \equiv A(\xi)$$

exists (see [16]) and under mild technical conditions *variation,* $\delta A(\xi)$, with $\delta b = 0$ at time 0 and time S can be defined whose *vanishing yields* the famous *Newton-Nelson Equation.*

$$\tfrac{1}{2}\,(DD_* + D_*D)(\xi(s)) = -\,\text{grad}_g V(\xi(s)). \tag{28}$$

The velocity $b(y, s)$ is a *control* with (28) its defining its *control equation* [16]. Equation (28) is the Stochastic Hamilton-Jacobi equation for the stochastic variation of $A(\xi)$.

Here,

$$DY \equiv \lim_{h\to 0} \tfrac{1}{h}\, \mathbb{E}\{Y(s+h) - Y(s)|\mathcal{P}_s\}$$

and

$$D_*Y \equiv \lim_{h\to 0} \tfrac{1}{h}\, \mathbb{E}\{Y(s) - Y(s-h)|\mathcal{F}_s\}$$

where $\mathcal{P}_s$ and $\mathcal{F}_s$ are the past and future σ-algebras: $\mathcal{P}_s \equiv \sigma\{\xi(t)|s \leq t\}$, $\mathcal{F}_s \equiv \sigma\{\xi(u)|u \geq s\}$.

The most powerful formulation of $\delta A(\xi(s)) = 0$ is due to Guerra-Morato-Nelson (see [16], [19]), and leads to curvature corrections in the explicit calculation of D and D_*. This leads to an equivalence of (28) with "Schrödinger's Equation"

$$i\nu \, \frac{\partial \psi}{\partial s}(y,s) = \big[- \, \frac{\nu^2}{2} \, \Delta_g + V(y) - \, \frac{\nu^2}{12} \, R \big] \psi(y,s),$$

where $i = \sqrt{-1}$ and R is Riemann scaler curvature, see [17], and

$$\begin{aligned} b(y,s) &= \nu(I_m + R_e) \, \frac{\mathrm{grad}_g \psi(y,s)}{\psi(y,s)} \,, \\ \rho(y,s) &= |\psi(y,s)|^2, \quad \text{complex modulus.} \end{aligned}$$

Stationary Solutions are of the form

$$\psi(y,s) = [\exp{(-i\lambda s)}]\varphi_\lambda(y) \tag{29}$$

and solve the eigenvalue problem

$$\lambda \varphi_\lambda(y) = - \, \frac{\nu^2}{2} \, \Delta_g \varphi_\lambda(y) + V(y)\varphi_\lambda(y) - \, \frac{\nu^2}{12} \, R\varphi_\lambda(y) \tag{30}$$

where R is the Riemannian scalar curvature of the Riemannian geometry defined by $ds^2 = \sum\limits_{i,j=1}^{n} g_{ij} dx^i dx^j$.

For our ($n = 2$) case, we have $R \equiv 0$ and may use (27) as a starting point without loss of generality and obtain for (30) the equation

$$- \, \tfrac{1}{2} \, \nu^2 \Delta_{\text{polar}} \varphi(r) + \tfrac{k}{2} \, r^2 \varphi_\lambda(r) = \lambda \varphi_\lambda(r) \tag{31}$$

where $k = a(\alpha_1^2 + \alpha_2^2)$. This is a *discrete spectrum* problem whose *lowest eigenvalue* is $\lambda_p \equiv \lambda_0$,

$$\lambda_0 = \Big[\frac{\nu^2 k}{\alpha_1^2 + \alpha_2^2}\Big]^{1/2}$$

and whose corresponding eigendensity is (following Nagasawa [18])

$$\varphi_0(r) = C_0^2 \, \exp\Big\{ - \Big[\frac{k}{\nu(\alpha_1^2 + \alpha_2^2)}\Big]^{1/2} r^2 \Big\}$$

and is clearly Gaussian. In general, $\lambda_p = (p+1)\lambda_0$ and their corresponding eigendensity are many. For instance, for $p = 2$

$$\begin{aligned} \varphi_{20} &= C_2^2 [\alpha(\overline{y}^1)^2 - \tfrac{1}{2}]^2 e(r) \\ \varphi_{02} &= C_2^2 [\alpha(\overline{y}^2)^2 - \tfrac{1}{2}]^2 e(r) \qquad (r^2 = (\overline{y}^1)^2 + \overline{y}^2)^2) \\ \varphi_{11} &= C_2^2 \alpha \overline{y}^1 \overline{y}^2 e(r) \end{aligned}$$

where $\alpha^2 = k/\nu(\alpha_1^2 + \alpha_2^2)$ and $\overline{y}^1, \overline{y}^2$ are rectangular Cartesian coordinates; the function

$$e(r) = \; \exp\Big\{ - \Big[\frac{k}{\nu(\alpha_1^2 + \alpha_2^2)}\Big]^{1/2} r^2 \Big\}.$$

In general, we have *nodal lines* defined in y^1, y^2 space by $\varphi_\lambda \equiv 0$. No sample path $\xi(s)$ of a Nelson process (28) can every reach one of these lines (i.e. the event has probability zero).

Yet, within the regions defined by all $\varphi_\lambda \equiv 0$, for fixed λ_p, the processes are ergodic, and their densities φ_λ are occuring in *discrete bounded parcels* and these do not communicate. Moreover, it is a basic theorem of Nelson Stochastic Mechanics that as $\nu \to 0$ sample paths of (28) converge to the deterministic paths solving the Euler-Lagrange equation (even for $V = 0$) for the *same* Lagrangian.

In (26) we rewrite to get

$$\frac{d^2y^i}{ds^2} = -\sum_{j,k=1}^{2} \Gamma^i_{jk} \frac{dy^i}{ds}\frac{dy^k}{ds} - a\alpha_i, \quad i = 1, 2. \tag{32}$$

In order to model a "noisy" environomental potential V we wish to add terms in y_1 and y_2, but such terms are *not* specified except that they take values in bounded intervals. Thus, the simplest modification of a "Taylor expansion" would be

$$V(y^1, y^2) = \tfrac{1}{2}\left(a + p_1(y^1) + p_2(y^2)\right)e^{2\phi(y^1,y^2)} \tag{33}$$

where

$$P_i \le p_i(y^i) \le P_i, \quad (i = 1, 2).$$

The $p_i(y_i)$ are only required to be absolutely continuous and the $P_i > 0$, are constants.

We further require the conditions

$$-\alpha_i R_i \le \tfrac{1}{2}\frac{\partial p_i}{\partial y^i} \le \alpha_i R_i \quad (i = 1, 2) \tag{34}$$

for positive constants, R_i. Clearly, we have

$$\begin{aligned} \alpha_1[a - P_1 - P_2 - R_1] \le\ & \mathrm{grad}^1_g V \le \alpha_1[a + P_1 + P_2 + R_1] \\ \alpha_2[a - P_1 - P_2 - R_2] \le\ & \mathrm{grad}^2_g V \le \alpha_1[a + P_1 + P_2 + R_2]. \end{aligned}$$

Considering (32) with potential (33) as a differential inclusion we have

$$\frac{d^2y^i}{ds^2} \in -\sum_{j,k=1}^{2} \Gamma^i_{jk} \frac{dy^j}{ds}\frac{dy^k}{ds} - \alpha_i[a - P_1 - P_2 - R_i, a + P_1 + P_2 + R_i], \quad i = 1, 2. \tag{35}$$

For system (35) we define maximal and minimal solutions $(y^*)^i, (y_*)^i$, $i = 1, 2$ to be solutions of the following differential equations:

$$\frac{d^2(y_*)^i}{ds^2} = -\sum_{j,k=1}^{2} \Gamma^i_{jk} \frac{d(y_*)^j}{ds}\frac{d(y_*)^k}{ds} + \alpha_i(a + P_1 + P_2 + R_i), \ i = 1, 2 \tag{36}$$

$$\frac{d^2(y^*)^i}{ds^2} = -\sum_{j,k=1}^{2} \Gamma^i_{jk} \frac{d(y^*)^j}{ds}\frac{d(y^*)^k}{ds} - \alpha_i(a - P_1 - P_2 - R_i), \ i = 1, 2. \tag{37}$$

Let us note that any solution $y(\cdot)$ of (35) satisfies $y_*(t) \le y(t) \le y^*(t)$ for every $t \ge 0$.

Following transformation via

$$\begin{aligned} \xi^1 &= e^{\phi(y^1,y^2)}\cos(\alpha_2 y^1 - \alpha_1 y^2) \\ \xi^2 &= e^{\phi(y^1,y^2)}\sin(\alpha_2 y^1 - \alpha_1 y^2), \end{aligned}$$

we transform (36) and (37) to

$$\frac{d^2(\xi^*)^i}{ds^2} = -[a + P_1 + P_2 + R_i](\xi^*)^i, \quad i = 1, 2$$

$$\frac{d^2(\xi_*)^i}{ds^2} = -[a - P_1 - P_2 - R_i](\xi_*)^i, \quad i = 1, 2$$

as long as $R_1 = R_2$. These are equations of 2 independent harmonic oscillators, therefore ξ^* and ξ_* are bounded and thus, all solutions of (32) are *canalized*, or in other words, growth of the clone is targeted for biomass, as we wished to show.

5. FINAL REMARKS

We have seen that fuzzy noise theory can be implemented in cases where there is no appropriate stochastic theory and that even the sophisticated Nelson stochastic mechanics, appropriate for some conservative problems in biology, can be considerably simplified with fuzzy Nelson mechanics. But, as yet there is no fuzzy theory which yields a discrete spectrum eigenvalue problem as in the stochastic Nelson theory. The authors think this is the most outstanding open question suggested by the present paper.

ACKNOWLEDGEMENTS

The authors would like to give special thanks to Vivian Spak for her unbounded patience and excellent AMS-TEX typesetting.

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