THE INSTITUTE OF STATISTICS

UNIVERSITY OF NORTH CAROLINA SYSTEM

ABSTRACTS OF CONTRIBUTED PAPERS FOR NSF-CBMS CONFERENCE ON "STOCHASTIC PROCESSES IN THE NEUROSCIENCES"

North Carolina State University

June 23-27, 1986

Compiled by

Charles E. Smith and Nancy Evans

Institute of Statistics Mimeo Series #1693

Biomathematics Series No. 28

NORTH CAROLINA STATE UNIVERSITY
Raleigh, North Carolina

ABSTRACTS OF CONTRIBUTED PAPERS FOR NSF-CBMS CONFERENCE ON "STOCHASTIC PROCESSES IN THE NEUROSCIENCES",

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An NSF Conference Board of Mathematical Sciences Regional Conference on "Stochastic Processes in the Neurosciences" was held at North Carolina State Univ. during June 23-27, 1986. Henry C. Tuckwell of Monash Univ., Dept. of Mathematics, was the principal lecturer. Schedules of his talks, the invited talks, and contributed talks are given below. Thirty-two scientists (mathematicians, statisticians, neurobiologists) attended the conference as formal participants.

A manuscript based on the 10 lectures below is being prepared by the principal lecturer, Henry Tuckwell. The three invited talks will appear in the Journal of Theoretical Neurobiology. Abstracts of the contributed talks are given here. Also included are a list of participants and the abstracts for a special Biomathematics seminar on "Optimal Harvesting and Pest Control" by two of the conference participants.

PRINCIPAL LECTURER'S 10-LECTURE PROGRAM

L1. Historical review. A brief survey of the deterministic background including mapping procedures for the dendritic trees.

L2. Random walk models.

L3. Discontinuous Markov models.

L4. Diffusion approximations.

L5. Stochastic partial differential equations.

L6. The analysis of stochastic neuronal activity.

L7. Channel noise.

L8. Wiener Kernel expansions.

L9. Further results for neural models.

L10. Analysis of the stochastic activity of neuronal populations.

Each lecture was approximately one hour, followed by a question and discussion period.

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SCHEDULE FOR INVITED TALKS

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TUESDAY June 24
1:30 G. Kallianpur (UNC)
Stochastic Differential Equation Models for Spatially Distributed Neurons.

WEDNESDAY June 25
9:00 John Walsh (Univ. British Columbia)
A Stochastic Model of Neural Response.

THURSDAY June 26
10:30 Grace L. Yang (Univ Maryland)
Modeling of Sodium Channel Conductance, and Estimation of Parameters.

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SCHEDULE FOR CONTRIBUTED TALKS

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MONDAY June 23 Chair: Dennis Ryan, Wright State Univ.
3:00 Davis Cope (North Dakota State Univ.)
Numerical solution of differential-difference equations with backward and forward differences.

3:25 Marjo V. Smith (UNC)
A numerical method for use with nonlinear stochastic differential equations.

3:50 Floyd Hanson (Univ of Illinois-Chicago)
Poisson stochastic differential equation models.

4:15 G. Rajamannar (Concordia Univ)
Renewal point processes and neuronal spike trains.

TUESDAY June 24 Chair: G. Kallianpur, UNC
3:30 George Adomian (Univ. of Georgia)
Analytic solutions of nonlinear stochastic systems of partial differential equations.

3:55 Shunsuke Sato (Osaka Univ.)
On a diffusion approximation of stochastic activities of a single neuron.

4:20 Petr Lánský (Czech. Academy of Sciences)
Diffusion approximations of the neuronal model with reversal potentials.

4:45 S. Ramaswamy (UNC)
Radonifying maps and infinite dimensional stochastic processes.

WEDNESDAY June 25 Chair: M. K. Habib, UNC
3:00 P. K. Sen (UNC)
Bootstrap procedures for cross correlation studies.

3:25 Roger Gaumond (Penn State)
Relative frequency estimates of AP discharge probability.

3:50 Edward Chornoboy (Johns Hopkins)
Examples of maximum likelihood techniques for neural point processes.

4:15 Ian W. McKeague (Florida State Univ.)
Inference for a semimartingale regression model using the method of sieves.

4:40 S. T. Chiu (Rice Univ.)
Regression on discontinuous curves.

THURSDAY June 26 Chair: James Koziol, Scripps Clinic
1:30 John Clay (NIH-Woods Hole)
Membrane noise in nerve and cardiac cells.

1:55 M. W. Levine (Univ. of Illinois-Chicago)
A model for the generation of the maintained discharges of retinal ganglion cells.

2:20 Charles E. Smith (NCSU)
A stochastic version of Kernell's afterhyperpolarization model.

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THURSDAY EVENING NCSU Faculty Club

PANEL DISCUSSION:
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Wiener Kernel Expansions: Domain of Applicability and Validity
Moderator: H. C. Tuckwell (Monash Univ.)
Panel: G. Kallianpur (UNC)
John Walsh (Univ. British Columbia)

Analysis of Recordings from More than One Neuron
Moderator: J. Sethuraman (Florida State Univ.)
Panel: P. K. Sen (UNC)
Roger Gaumond (Penn State)
Brian Rasnow (CALTECH)

Analysis and Models of Membrane Noise
Moderator: Grace L. Yang (Univ Maryland)
Panel: Harold Lecar (UC-Berkeley)
John Clay (NIH-Woods Hole)

A New Approach to Neurological Models

G. Adomian

Modeling and analysis of biological problems involving response and interactions in physiological systems may possibly benefit from a methodology (1) which has been applied successfully to a number of physical problems (2). Neural networks display nonlinearity and stochasticity as essential features in their processing and transmission of information. Common mathematical procedures such as linearization can change the physical results significantly — so that the system solved can be quite different than the original nonlinear model. Randomness is also present in real systems - either in parameters of an individual system or in equations involving variations from one individual to another. Mathematical treatment usually restricts either the magnitude of the fluctuations or their nature. Thus it is desirable to avoid perturbation, hierarchy methods (truncations), white noise, etc. and assume general stochastic processes with physically realistic correlation functions. The method we will use in the decomposition method — allows us to obtain solutions for real nonlinear stochastic problems rather than simplified linearized or averaged problems. It allows solutions of a wide class of equations in a generally rapidly converging series form. These equations include systems of ordinary or partial differential equations which can be strongly nonlinear and/or stochastic, and involve linear, nonlinear, or coupled boundary conditions as well as including constant, time-dependent, or random delay terms . Modeling is always a compromise between mathematical tractability and realistic representation. With fewer limitations imposed to achieve tractability, models can be made more physically realistic. Less work and more insight into the problem is obtained than with massive numerical computations.

1) Nonlinear Stochastic Operations Euations, G. Adomian, Academic Press 1986 (available end of July.

2) Applications of Nonlinear Stochastic Operation Equations to Physics, G. Adomian (expected end of 1986).

Center for Applied Mathematics, University of Georgia, Athens, GA 30602

Note: There are two earlier books (Stochastic Systems, G. Adomian, Academic Press 1983 and Partial Differential Equations - New Methods for Their Treatment and Applications, R. E. Bellman and G. Adomian, Reidel 1985.

Examples of Maximum Likelihood Techniques for Neural Point Processes

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Determination of the functional relationship bewteen neural point processes has, in the past, relied on fitting models to estimated moment functions (method of moments). An *invariant* characterization, using this technique, requires severe assumptions and thereby limits the scope of its application. In particular, system "inputs" must be realizations from independent Poisson processes and the system to be characterized is assumed to be "open loop".

Using recent developments that involve the representation of point processes via their stochastic intensities, we have begun to explore the application of maximum likelihood techniques to the problem of neural systems identification. We have considered the n-dimensional point process system $N=[N_1,\ldots,N_n]^T$ where each component process is assumed to possess stochastic intensity $\lambda_i(t)$ which is modeled by a finite sum of Volterra integrals:

$$\lambda_i(t)=k_{0i}+\sum_{j=1}^{n}\int_0^t k_{1ij}(t-u)N_j(du)+\sum_{j=1}^{n}\sum_{l=1}^{n}\int_0^t\int_0^t k_{2ijl}(t-u,t-v)N_j(du)N_l(dv).$$

The kernels are approximated by piecewise constant functions and maximum likelihood estimates for the approximating functions are obtained iteratively by applying the EM algorithm of Dempster, Laird, and Rubin (J. Roy. Stat. Soc., Ser. B, 39, 1977).

Numerical convergence of the EM algorithm for this application have been found to be excellent. Satisfactory estimates have been obtained within 10-12 iterations, irrespective of the data sample or model order. Therefore, the maximum likelihood method expands the class of neural systems which may be studied using the above model. Using this method, systems with non-stationary inputs and systems with feedback can be studied.

Regression on Discontinuous Curves

By Shean-Tsong Chiu

Rice University

Abstract

A smoothing method for discontinuous curves is presented. The procedure can preserve the discontinuities of the curve, it can also detect the outliers. The procedure is applied to the data set consisting of intervals between coal-mining disasters.

Numerical Solution of Differential-Difference Equations with Backward and Forward Differences

Davis Cope

Equations of this type occur in determining the moments for interspike times in neuron models with Poisson excitation and inhibition. We discuss a recursion procedure which refines an initial approximation to an appropriate smooth solution.

MEMBRANE NOISE IN NERVE AND CARDIAC CELLS

John R. Clay

Fluctuations in membrane excitability will be described in small clusters of chick embryonic heart cells. These preparations beat spontaneously with an interbeat interval which is independent of the number of cells in the cluster. The coefficient of variation in beat rate varies inversely as the square root of the number of cells. These results can be modeled by a random walk with linear drift to threshold.

A second topic of discussion in this talk concerns simulations of excitability in a patch of nerve membrane containing a small number of sodium and potassium channels described by Hodgkin - Huxley kinetics. The first passage time to threshold was calculated from these simulations as a function of the size of the patch, A, keeping channel density constant. The mean first passage time was independent of patch size, whereas the coefficient of variabation varied as $A^{-1/2}$.

RELATIVE FREQUENCY ESTIMATES OF AP DISCHARGE PROBABILITY

R. P. Gaumond and R. B. Richard

Bioengineering Program, The Pennsylvania State University

We have investigated methods of extracting <u>relative frequency estimates</u> of AP discharge probability for each of several interacting neurons in multi-neuron AP recordings. Application of these methods to the analysis of AP data from single cochlear nerve fibers was described in Gaumond, Molnar, and Kim (1982).

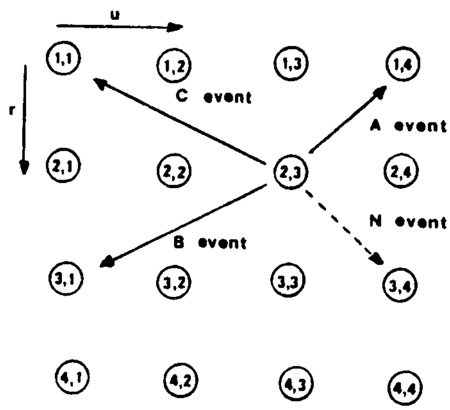
Consider AP spike discharge waveforms recorded simultaneously from two neurons. Divide the recording epoch into time increments Δt, where Δt is small enough that no one neuron can discharge twice during a single increment Δt. With this restriction, there are only four possible events which can occur during any increment:

A event: neuron A discharges, not B
B event: neuron B discharges, not A
C event: both A and B discharge
N event: neither A nor B discharges

Let r and u be positive integer valued state variables associated with each time increment Δt, where r is the number of increments since the previous discharge of neuron A, and u is the number of increments since the previous discharge of neuron B. Let A(r,u) be the number of A events in all increments Δt of a continuous two-neuron AP discharge record. Similar definitions apply to B(r,u), C(r,u), N(r,u) and to T(r,u)=A(r,u)+B(r,u)+C(r,u)+N(r,u). Then $P_A(r,u)$, a relative frequency estimate of the discharge probability of neuron A conditional on state variables r and u, is given by:

$$P_A(r,u) = (A(r,u)+C(r,u))/T(r,u) \qquad (1)$$

Computation of A(r,u), B(r,u), C(r,u) and T(r,u) could, in principle, proceed by incrementing the proper counter after noting which event type occured durnig each Δt. However, a substantial reduction in compputation time may be achieved by noting the interdependence of these quantities. The accompanying figure shows an explicit Markov Chain model structure for the situation where state variables r and u determine all state transition probabilities. u increases to the right while r increases in a downward direction. At the beginning of each time increment Δt, the neuronal system is said to be in one state of this model (e.g., state (2,3)) and to move to one of 4 possible new states by the end of Δt. In any lengthy sequence of discharge transitions which does not begin or end in state (r,u+1) the following must be true:



$$T(r,u+1)=T(r,u)-A(r,u)-B(r,u)-C(r,u) \qquad (2)$$

Use of equation (2) generally allows computation of the relative frequency estimates of equation (1) from counts of the number of A, B and C events corresponding to each state variable pair. Since, for small Δt, N events predominate in the discharge record, the savings in computation time is significant.

It is easily shown that expressions of the form of equation (1) provide maximum likelihood estimates of state transition probabilities defining the Markov Chain model shown above, and that the joint distribution of the random variables A(r,u), B(r,u), C(r,u) and N(r,u) is multinomial, conditional on the value of T(r,u). It is straightforward in principle to extend these concepts to situations in which additional state variables are considered. For example, a variable corresponding to the time-since a periodic stimulus marker can be included as an additional state variable. However, the storage required for event counts increases as the product of the number of state variables, and may impose practical limits to use of this procedure.

Reference:

Gaumond, R. P., Molnar, C. E. and Kim, D. O. (1982). Stimulus and recovery dependence of cat cochlear nerve fiber spike discharge probability. J. Neurophysiol. 48:856-873.

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POISSON STOCHASTIC DIFFERENTIAL EQUATION MODELS

Floyd Hanson
University of Illinois at Chicago
and
Argonne National Laboratory

A selected survey of Poisson SDE models is given. An application of distributed Poisson models is presented for the postsynaptic response to MEPP's at a neuro-neuron junction. This model is motivated by the multi-vesicle theory. Preliminary asymptotic results are given for a diffusion approximation of the ISI distribution.

DIFFUSION APPROXIMATIONS OF THE NEURONAL MODEL WITH REVERSAL POTENTIALS

Petr Lánský
Institute of Physiology
Czechoslovak Academy of Sciences, Prague

The stochastic neuronal model with reversal potentials is approximated either by a deterministic model or by a diffusion process. For the model with constant postsynaptic potential amplitudes a deterministic approximation is the only one which can be applied. This deterministic model is different from those usually used in that the leakage term is influenced by the input processes. The diffusion approximations are performed under the condition of random postsynaptic potential amplitudes. The new diffusion models for nerve mebrane potential are devised in this way. These new models are more convenient for an analytical treatment than the original one with discontinuous trajectories. Also the parameters of the diffusion models can be more easily estimated. The maximum likelihood method is illustrated on one case as an example.

A MODEL FOR THE GENERATION OF THE MAINTAINED DISCHARGES OF RETINAL GANGLION CELLS

Michael W. Levine

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A model that can account for the statistics of the maintained discharges of goldfish and cat ganglion cells is presented. The basic model consists of an integrate-and-fire mechanism, which integrates a variable signal until a threshold for impulse production is reached. The variable signal is white noise, distributed according to either a Gaussian or a gamma distribution.

Interval distributions from ganglion cell maintained discharges may be fit with a "hyperbolic normal" distribution, but are generally better fit with a "hyperbolic gamma" distribution. However, the interval distributions generated by the models demonstrate that this need not imply a skewed variable signal.

Temporal dependencies (autocorrelation) in the firing are easily demonstrated by plotting the standard deviation of the firing rate versus the duration of the samples from which it was calculated. This method reveals considerable high-pass filtering in the maintained discharges of fish ganglion cells, and minimal high-pass filtering in those of the cat. A model in which the variable signal passes through a band-pass filter (the transfer function for photic signals) produces discharges with a stronger high-pass characteristic than even that of the fish. This characteristic may be mitigated by adding white noise to the filtered signal.

One of the original requirements of the model had been that the coefficient of variation of the firing be independent of the mean firing rate. Newer data indicate that the coefficient of variation declines with increases in firing rate. With an appropriate choice of which parameter effects changes in mean firing rate, the model predicts that the coefficient of variation should be inversely proportional to the square root of the firing rate. This is a reasonable first approximation to the data, but not exactly correct.

INFERENCE FOR A SEMIMARTINGALE REGRESSION MODEL USING THE METHOD OF SIEVES

Ian W. McKeague

Florida State University

Estimation for a nonparametric regression model for semimartingales is studied. The model is given by $X(t) = \int_0^t \lambda(s)ds + M(t)$, $t \in [0,1]$, where M is a martingale and $\lambda(s) = \sum_{j=1}^p \alpha_j(s)Y_j(s)$. Here $\alpha_1,\ldots,\alpha_p$ are deterministic functions of time and $Y_1,\ldots,Y_p$ are observable covariate processes. This model was introduced by Aalen (LECTURE NOTES IN STATISTICS 2(1980) 1-25 Springer-Verlag) in a counting process setting as an alternative to the Cox regression model for the analysis of censored survival data. Grenander's method of sieves is applied to obtain estimators of $\alpha_1,\ldots,\alpha_p$ from iid observations of X and its covariates. The asymptotic distribution theory of these estimators is developed and a variety of applications are discussed.

RENEWAL POINT PROCESSES AND NEURONAL SPIKE TRAINS

G. RAJAMANNAR

Concordia University

The mechanism of formation of the single neuronal spike trains is explained as a result of certain type of interaction between two independent stationary point processes. The different kinds of interactions that have been used in this context are reviewed.

S. RAMASWAMY (UNC Center for Stochastic Processes)

Radonifying maps and infinite dimensional stochastic processes

Abstract

The aim of the article and the talk is to apply some results of L. Schwartz's theory of Radonifying maps to prove some existence results for random variables with values in the dual of a nuclear space. More precisely, the result we prove is the following: Let E be a nuclear space and let ϕ be a continuous positive-definite kernel on ExE. Then $\exists$ a random variable X on some probability space (Ω, F, P) with values in E', the dual of E such that the family $(X_x)_{x \in E}$ of real random variables where $X_x(\cdot) = \langle x, X(\cdot)\rangle$ is a Gaussian family with covariance ϕ. (The $\langle , \rangle$ denotes the duality between E and E').

This result is already proved by K. Itô and M. Nawata in [1], by a different method.

1. K. Itô and M. Nawata: Regularization of linear random functionals. (Lecture Notes 1021, 1983).

On a Diffusion Approximation of Stochastic Activities of a Single Neuron

by Shunsuke Sato
Osaka University

Abstract:

The neuronal firing time is viewed as a first passage time of the membrane potential through generally time dependent neuronal threshold. In some neurons, the subliminal time course of the membrane potential sometimes varies irregularly as a reflection of the stochastic nature of the inputs, and hence is modeled as the diffusion process such as Ornstein-Uhlenbeck process. The first-passage-time probability density function thus provides us a description of the statistical features of the neuronal firing. In the present paper, we deal with the Ornstein-Uhlenbeck process model to account for the features. The p.d.f. of the first-passage-time to a constant boundary for the process starting from some initial value is considered using the Laplace transform technique. Both recursive and explicit expressions for the moments of the p.d.f. and asymptotic moments for a large value of the boundary are obtained. Several properties of the p.d.f. itself including its asymptotic form are also provided.

Bootstrap Procedures for Cross-Correlation Studies

Pranab K. Sen and Muhammud K. Habib
University of North Carolina, Chapel Hill.

For the study of the association patterns of spike trains recorded simultaneously for two or more neurons, often, first and second order stationarity assumptions are not tenable, and one needs to consider more general methods which allow for plausible non-stationarity. Cross correlation surfaces have been studied by Habib and Sen (1985) and others, and these appear to have some distinct advantages over the usual lag-correlations. For doubly-stochastic Poisson processes when the (marginal) intensity functions (though non-stationary) are low, the usual asymptotic theory developed in Habib and Sen (1985) may not be properly applicable unless one has a large number of replications. To overcome this difficulty, Bootstrap procedures are used to provide a simultaneous confidence region for the cross-correlations. In this scheme, instead of the usual Euclidean norm (or the Mahalanobis distance), 'max norm' is used. The immediate advantage is to eliminate the 'near singularity' effect which may have serious impact on the usual norms. Weak convergence of the Bootstrap empirical distribution (studied in this context) provides the desired solutions.

A STOCHASTIC VERSION OF KERNELL'S AFTERHYPERPOLARIZATION MODEL

Charles E. Smith
Department of Statistics, Biomathematics Division
North Carolina State University

Two stochastic one-compartment models for the production of action potentials are used to examine repetitive firing in the neurons of the mammalian balance organs (vestibular afferents). The times of occurrence of action potentials (firing times) can be viewed as the first passage times to an absorbing barrier, or "threshold". The first model is a nonlinear stochastic differential equation driven by both Poisson and Wiener processes. The moments of this process can be used to approximate the mean and variance of the firing times under certain conditions (Smith and Smith, 1984). The second model (Smith and Goldberg, 1986) is more realistic in that it has time-varying coefficients, in lieu of a time-varying absorbing barrier, and is driven by a shot noise process. While an analysis using approximation methods provides some insights, simulation results are used to make a detailed comparison to experimental data (Goldberg, Smith, Fernández, 1984). The model reproduces many features of the steady-state discharge of peripheral vestibular afferents, provided the firing rates are higher than 40 spikes/sec. Among the results accounted for are the interspike interval statistics during natural and electrical stimulation. Finally, for the second model, the resultant point process is not a renewal process. The nature of the serial order dependence is examined and suggestions are made for data analysis on the joint intervals.

REFERENCES

Goldberg, J.M., Smith, C.E., Fernández, C. (1984). Relation between discharge regularity and responses to externally applied galvanic currents in vestibular nerve afferents of the squirrel monkey. J. Neurophysiol. 51: 1236-1256.

Smith, C.E. and Goldberg, J.M. (1986). A stochastic afterhyperpolarization model of repetitive activity in vestibular afferents. Biological Cybernetics 54: 41-51.

Smith, C.E. and Smith, M.V. (1984). Moments of voltage trajectories of Stein's model with synaptic reversal potentials. J. Theor. Neurobiol. 3: 67-77.

ABSTRACT

A NUMERICAL METHOD FOR USE WITH NONLINEAR STOCHASTIC DIFFERENTIAL EQUATIONS.

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The objective of this paper is to show how numerical approximation to sample paths of a stochastic differential equation can be converted into an approximation to the probability distribution of the state variable $X(t)$ as a function of time t. In a case where the result is known analytically, it is shown how well this approach works by comparing its results to the analytical ones. Then the method is used to explore some stochastic differential equations of applied interest for which no analytical results are available.

BIOMATHEMATICS GRADUATE PROGRAM - NCSU

Special Seminar on

"Optimal Harvesting and Optimal Pest Control"

SPEAKERS

Dr. Dennis Ryan
Department of Mathematics and Statistics
Wright State University
Dayton, OH

Title of Talk: "Optimal Harvesting of a Logistic Population in an Environment with Stochastic Jumps."

Dr. Wenyaw Chan
Department of Mathematics and Statistics
Case Western Reserve University
Cleveland, OH

Title of Talk: "Optimal Pest Control for a Stochastic Pest-Predator Model."

Thursday, June 26, 1986

3:30 p.m.

209 Cox Hall

OPTIMAL HARVESTING OF A LOGISTIC POPULATION IN AN ENVIRONMENT WITH STOCHASTIC JUMPS

Dennis Ryan
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Wright State University
Dayton, Ohio 45435

ABSTRACT

Dynamic programming is employed to examine the effects of large, sudden changes in population size on the optimal harvest strategy of an exploited resource population. These changes are either adverse or favorable and are assumed to occur at times of events of a Poisson process. The amplitude of these jumps is assumed to be density independent. In between the jumps the population is assumed to grow logistically. The Bellman equation for the optimal discounted present value is solved numerically and the optimal feedback control computed for the random jump model. The results are compared to the corresponding results for the quasi-deterministic approximation. In addition, the sensitivity of the results to the discount rate, the total jump rate and the quadratic cost factor is investigated. The optimal results are most strongly sensitive to the rate of stochastic jumps and to the quadratic cost factor to a lesser extent when the deterministic bioeconomic parameters are taken from aggregate antarctic pelagic whaling data.

OPTIMAL PEST CONTROL FOR A STOCHASTIC PEST-PREDATOR MODEL

by

Wenyaw Chan

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ABSTRACT

A pest-predator stochastic model proposed by Bartoszyński [1] is adapted to cover control variables such as the death rate of the pest due to pesticide and the size of the predator population. The model assumes that the pest population is influenced by the predation and can only increase at breeding seasons and that the predator population follows a linear birth-and-death process. Under the assumption of a fixed and non-transferrable budget, this paper seeks to find an optimal policy for determining the best allocation of resources between buying new predators and buying pesticides. The criteria to be optimized involve: (1) the probability that the pest population will be extinguished by a target time, (2) the expected accumulated sum of the pest population by a target time and (3) the total discounted sum of pest population in the future.

1. R. Bartoszyński, On chances of survival under predation. Math. Biosci. 33: 135-144 (1977).

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