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INTRODUCTION

This continues the biennial (approximately) update of the series begun in 1978. As this issue attests, there is biomathematical work in many parts of the North Carolina State University campus. This issue contains contributions from 18 departments in the Schools of Agriculture and Life Science, of Physical and Mathematical Sciences, of Forest Resources, and of Veterinary Medicine. The primary function of the series has been to serve as a basis for communication. Users of previous editions will note that the name has been altered to more appropriately reflect the community being served.

There are no clear boundaries as to what type of work should be included in such a collection. Most biological research will have some mathematical content, and most work in mathematical science is at least potentially applicable to biology. The intent is to include biological work in which mathematical methods play a central role, and mathematical work of clear relevance to biology. Included are abstracts of published work, and descriptions of work in progress.

The subject index is compiled in terms of broad subject matter categories. In most cases, the keywords for the index were supplied by the contributor.

I should like to express appreciation to Nancy K. Evans, who not only did the physical preparation of this booklet, but who shared in the design of the format, and was responsible for details of organization and production, for gently coaxing late contributors, and in general, for keeping the project on track.

As before, suggestions for improving the usefulness of future editions would be warmly welcomed.

Harvey J. Gold
Director
Biomathematics Graduate Program

November 1983.
# LISTING BY DEPARTMENT

Note: underlining indicates department affiliation, and a "*" indicates Biomathematics Graduate Program faculty. Entries with authors from several departments are listed under each department.

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VETERINARY MICROBIOLOGY, PATHOLOGY AND PARASITOLOGY
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A METHOD FOR DESCRIBING THE EFFECTS OF GENOTYPE AND DAILY INTAKE ON TOTAL DAILY GAIN DURING POSTWEANING GROWTH IN CATTLE

E. A. Tolley and M. W. Tess
Department of Animal Science

T. Johnson
Departments of Business and Economics, and Statistics

Data obtained from the scientific literature were used to develop a method for determining mathematical curves for describing the effects of genotype and daily energy intake (EI) on total daily gain (G) during postweaning growth of cattle when sex and time of feed were varied. If daily protein accretion (P) in kg is related to total daily gain (G) in kg by a Brody function, \( P = \alpha (1 - \beta e^{-\gamma G}) \). Then through the energy balance relationship, protein gain is the following implicit function of total gain: \( G = \theta_0 + \theta_1 \ln(\alpha' - C_P P) + \theta_4 P \), where \( \theta_0 = \frac{1}{-C_F} \ln \frac{1}{\alpha' \beta'} + \frac{1}{-C_F} \theta_1 = \frac{C_P}{C_F} \), \( \theta_4 = 1 - \frac{C_P}{C_F} \), and \( C_P \) and \( C_F \) are the heat combustion values for protein and fat, respectively. Daily protein accretion and daily intake may be expressed in terms of energy as \( R_E P = \alpha' (1 - \beta' e^{-\gamma' R_E}) \) and \( EI = M + b_F R_E F + b_P R_E P \), where \( R_E P = \) daily rate protein deposition (Mcal); \( R_E = \) daily rate energy retention (Mcal); \( EI = f(\text{genotype, environment}) = \) daily rate energy intake (Mcal); \( M = \) maintenance requirement (Mcal); \( R_E F = \) daily rate fat deposition (Mcal); and \( b = \) energy cost of fat (F) and protein (P) deposition (Mcal/Mcal), respectively. Substituting, growth in terms of energy may be graphically depicted by the explicit function \( EI = M + b_F R_E + \alpha' (b_P - b_F) (1 - \beta' e^{-\gamma' R_E}) \). When \( R_E = 0 \), \( EI = M + \alpha' (b_P - b_F) (1 - \beta') \). The asymptote has a slope of \( b_F \) and intercept of \( M + \alpha' (b_P - b_F) \). The cumulative energy intake (Mcal) over a given time period may be expended for maintenance over the time period, weight gain and change in composition. Thus, \( E = B_0 + B_1 W + B_2 e^{-B_3 W} \) where \( E = \) cumulative energy intake (Mcal) and \( W = \) empty body weight gain (Kg).
THE EFFECTS OF GENOTYPE AND RATE OF GAIN ON COMPOSITION OF POSTWEANING GROWTH IN CATTLE

E. A. Tolley and M. W. Tess
Department of Animal Science

T. Johnson
Departments of Business and Economics, and Statistics

Data obtained from the scientific literature were used to investigate mathematical curves describing the effect of rate of total daily gain (G) on daily protein accretion (P) and daily lean tissue deposition (L) during postweaning growth. For each dependent variable, four distinct curves sufficiently described three-dimensional response surface changes for either genotype or length of feeding period when the remaining fourth-dimensional variable (time or genotype) was held constant. A Laguerre polynomial,

\[ Y = B_0 + B_1 e^{-kG} + B_2 e^{-kG} + B_3 e^{-kG} \]

where \( Y = P \) or \( L \), \( B_0, B_1, B_2, B_3 \) are coefficients, and \(-kG\) is an exponent, was used to test alternative hypotheses related to the adequacy of three proposed growth models:

1. \[ Y = B_0 + B_1 e^{-kG} \] where \( B_1 = -B_0 \) (a Brody form);
2. \[ Y = A_0 + B_2 G \] where \( A_0 = B_0 + B_1 \); and
3. \[ Y = A_0 + B_2 G + B_3 G^2 \] where \( A_0 = B_0 + B_1 \).

With these data, neither nonlinear growth functions in the Brody form (Model 1) nor linear growth functions (Model 2) could be rejected in favor of the quadratic growth functions (Model 3). Model 1 was preferred because it may be interpreted mechanistically and can be used to obtain meaningful extrapolations from the observations.
Effect of Tissue Absorption and Microscope Optical Parameters on the Depth of Penetration for Fluorescence and Reflectance Measurements of Tissue Samples

Douglas M. Benson and James A. Knopp
Department of Biochemistry

Submitted to Photochemistry & Photobiology

An equation has been derived that is concerned with the measurements of fluorescence or reflectance intensities in reflectance or incident light microscopy. A theoretical basis for the linear relationship between relative fluorescence and reflectance changes is given. This equation predicts both the contributions of different volume elements below the surface of a tissue sample to the total intensity and the depth of penetration of the measured intensities. The relationship requires knowledge of the effective focal points of the excitation beam and the apparent absorption coefficient of the sample. Two procedures are given to provide the empirical values of the effective focal point. The absorption coefficient of mouse liver tissue at 420 nm was determined to be 3.3/mm. The fluorescence intensities of liver slices of differing thickness containing pyrene butyric acid were measured and were found to compare favorably with the calculated values for tissue absorption of 3/mm.
EVAPOTRANSPIRATION IN THE PRESENCE OF A WATER TABLE

M. Afiatouni
Biological and Agricultural Engineering Department

Experiments were conducted in 1980 and 1981 to evaluate the effects of root zone and water table depths on the evapotranspiration, ET, in the presence of a water table. An ET model was developed which took into account factors such as: 1) soil water availability in the root zone, 2) upward flux from the water table, 3) root water extraction pattern and crop growth stage, and 4) soil surface conditions. The model was tested using input data obtained from a controlled water table experiment in 50-cm-diameter soil columns exposed to natural conditions. Predicted weekly ET rates were in good agreement with the measured values obtained in the water table experiment.

Upward flux from the water table provided more than 80% of the total ET for all treatments. Shallow water table depths combined with deeper root depths resulted in the highest ET rates.

Experiments in the growth chamber were also conducted to measure the steady state ET rate for various water table depths. Results showed that the external potential demand governed the ET rate for water table depths near the soil surface; but, for deep water tables, steady ET was limited by soil profile factors such as depth to the water table and unsaturated hydraulic conductivity.

The ET model was incorporated into a water management model, DRAINMOD, and was applied to field situations using five years of experimental data from an eastern North Carolina site. The new ET model had a significant effect on the water table fluctuations during dry periods; but it did not have any effect during the wet conditions.
ECONOMICS OF UTILIZING LIQUID SWINE MANURE AS FERTILIZER

James C. Barker, Charles K. Allred, and Henry Y. R. Chen
Department of Biological and Agricultural Engineering

A microcomputer simulation of a liquid slurry system for handling the wastes generated by swine confinement production units is utilized to determine the economics of substituting these wastes for commercial fertilizer. The model addresses such information as the total amount of wastes generated annually from the production unit; the total and plant-available nutrient contents of the wastes; the size and costs of manure storage facilities; the number of acres that can be fertilized with manure based on crop fertilization recommendations as well as supplemental fertilizer required; the suggested sizes of pumping units and spreaders plus the corresponding tractor sizes; the total annual costs of manure storage facilities, handling equipment, and land spreading; and a cost comparison of fertilizing the same acreage with commercial fertilizer only.
A technique is developed for the analysis of plant growth in experiments where a one-time short-term stress (such as gaseous air pollution exposure) is applied during the ontogeny of the plant. The method is worked out in detail for the Richards growth function and applied to growth data of snap bean (Phaseolus vulgaris) exposed to ozone. This resulted in the value for the percent reduction in the growth rate (74% for the .60 ppm O₃ level) and an index for the recovery rate. Results from different studies are comparable.

The technique may also be utilized with effects other than stresses and multi-episodic and chronic events.
A MODEL OF CANOPY IRRADIANCE IN RELATION TO CHANGING LEAF AREA IN A PHYTOTRON-GROWN SNAP BEAN (PHASEOLUS VULGARIS L.) CROP

J. Heiner Lieth
U.S.D.A., Blackland Research Center, Temple, Texas

James F. Reynolds
Department of Botany


Simple exponential decay models were used to describe the variation in irradiance profiles within a snap bean (Phaseolus vulgaris L.) canopy over a 33-day period of canopy development. The extinction coefficients of these models were varied over time as a function of changing canopy leaf area; nonlinear least-squares procedures were used to estimate parameter values. The resultant model response surfaces depict the changes in canopy irradiance that accompany canopy maturation and illustrate the dynamic nature of canopy closure. A criterion index is defined to aid in assessing the applicability of these models for use in whole-plant simulation models, and an evaluation of these models is given based on this index, their predictive accuracy, and the utility for use within varying modeling frameworks.
A QUANTITATIVE STUDY OF VARIATION IN THE CHENOPODIUM
ATROVIRENS–DESICCatum–PRATERICOLA COMPLEX

James F. Reynolds
Department of Botany

Daniel J. Crawford
Department of Botany, Ohio State University, Columbus, Ohio 43210


Multivariate analyses were applied to 96 populations (OTUs) of plants, traditionally referred to Chenopodium atrovirens, C. desiccatum, and C. pratericola, in an attempt to evaluate the numerous and often contradictory taxonomic treatments of plants in this complex. The study consisted of two major parts. The first involved the use of cluster and principal components analyses using 14 morphological characters on the entire set of 96 OTUs to search for phenetically distinct groupings; these analyses were conducted without knowledge of traditional taxonomic designations of individual OTUs. Three reasonably well-defined groups emerged from these preliminary analyses. When traditional taxonomic designations were applied to member OTUs of each group, one group was composed primarily of C. atrovirens, another of C. pratericola and the third of C. desiccatum. The second part of the study utilized canonical analysis to: 1) confirm the integrity of the phenetic groups, 2) to classify OTUs difficult to identify to species using traditional methods, and 3) to provide an evaluation of characters important in the separation of these groups. This analysis confirmed the integrity of the groups and provided a classification to species of nearly all of the otherwise difficult OTUs. In addition, canonical analysis demonstrated that a combination of characters was important in the separation of the phenetic groups.
VALIDATION OF A PRIMARY PRODUCTION MODEL OF THE DESERT SHRUB
*Larrea tridentata* USING SOIL-MOISTURE AUGMENTATION EXPERIMENTS

James F. Reynolds
Department of Botany

Gary L. Cunningham
Biology Department, New Mexico State University,
Las Cruces, New Mexico 88003 USA


In previous papers we have describe and verified a primary production model of the desert shrub *Larrea tridentata*. Here we address the validation phase of the evaluation of this model. Two versions of the model which differ in the priority scheme used for allocating carbon to reproductive or vegetative organs were compared on the basis of their usefulness and reliability over a range of soil-moisture conditions. Over an entire growing season when soil-moisture conditions were near "normal" both versions of the model were adequate predictors of total above-ground vegetative growth and one was an adequate predictor of reproductive growth as well. A more detailed analysis revealed that the versions varied in the range of soil-moisture conditions over which they were adequate and that neither was adequate when soil-moisture had remained high for extended periods. The validation process has revealed some likely areas for model improvement to increase adequacy.
A MULTIVARIATE ANALYSIS OF THE PHOTOSYNTHETIC RESPONSES
OF SALTGRASS (DISTICHLIS SPICATA) TO IRRADIANCE,
TEMPERATURE AND SALINITY GROWTH TREATMENTS

James F. Reynolds
Department of Botany

Paul R. Kemp and Gary L. Cunningham
Department of Biology, New Mexico State University,
Las Cruces, NM 88003 USA

Photosynthetica (In Press)

The effects of growth irradiance, temperature, and salinity on net
photosynthesis and its partial process in Distichlis spicata were
investigated. This was accomplished by fitting parameters of a simple
gas-exchange model to photon fluence rate response data and examining the
pattern of treatment effects on the parameters using cluster, principal
component and variance analyses. Growth irradiance had its principal effect
on the incident photon-use efficiency. Temperature and salinity interacted to
influence the efficiency of carboxylation. Effects on stomatal responses
could not be separated from effects on carboxylation efficiency.
A SHOOT:ROOT PARTITIONING MODEL

James F. Reynolds
Department of Botany

John H. M. Thornley
Glasshouse Crops Research Institute, Littlehampton, West Sussex BN16 3PU


A model for partitioning newly-synthesized structural dry matter between shoot and root is developed. It is based on a postulated partitioning function, which depends upon the relative levels of carbon and nitrogen substrates, with parameters determining the control point and also the degree of control. The model is used to investigate the relationships between plant specific growth rate, shoot:root ratio, and the specific activities of shoot and root (which depend upon environment), during steady-state exponential growth; the transient behavior of the model is also explored and oscillations in these quantities are obtained.
Grass pasture swards are being harvested and stratified by cutting them into 5 cm layers. Strata begin 3-5 cm above the soil surface and continue to the extended height of the sward. The layers are then separated into leaf, stem, and dead material. Based upon the results of analysis for dry weight, carbohydrate fractions, in vitro dry matter disappearance (IVDMD), and Van Soest fiber fractions smooth curve reconstructions of the sward will be developed. Steers fitted with esophageal fistulas preference the swards and samples of extrusa are being collected. These samples will be analyzed for carbohydrate and fiber fractions, IVDMD, and leaf:stem:dead proportions, and the results used to construct a model which predicts the portion of a canopy consumed by a grazing steer. Comparisons will be made between the collected extrusa and available forage. Based upon literature values and animal intake (using markers) concurrent with sward stratification, the preference model will be coupled to the Mertens-Ely model of rumen function and evaluated.
MODELING PEANUT SEED LEACHING AS A FUNCTION OF SEED QUALITY

R. D. KEYS, DEPARTMENT OF CROP SCIENCE

The rapid and uniform assessment of peanut seed quality by seedsmen is a matter of fundamental commercial importance. Each year, several millions of dollars of peanut seed for planting seed stock (as opposed to edible stock) must be tested for "quality" according to various commercial and legal regulatory standards. The most common test in use from the commercial standpoint and the one mandated from the regulatory standpoint is the classical standard germination test. A problem that exists is that this test takes minimally 10 days plus some additional "turn-around" time, but seedsmen often need to know the "quality" of a particular lot of peanut seed in a matter of minutes or at most several hours, so that commercial handling decisions can be made. Recently, a quick seed quality test requiring only 3 hr. time, and based upon the classical observation that seed, when placed in water, leach materials inversely proportional to their quality, was developed here at NCSU\textsuperscript{1}. This test is fully automated, running under the control of a small microcomputer\textsuperscript{2}. To arrive at the greatest potential usefulness of this test, a working relationship of the rate of leaching of peanut seed vs. the standard germination of the seed needed to be developed. Several hundreds of commercial lots of peanut seed were tested over a three year period. The rate of leaching (efflux rate) and standard germination (% germination) values were taken. A functional model of efflux rate vs. % germination may be given as follows:

$$\text{efflux rate} = A - \% \text{germination}^B$$

For the peanut seed tested in North Carolina, the model developed was:

$$\text{efflux rate} = 1.65 - \% \text{germination}^{0.093}$$

Plotted graphically, the model can be used to quickly estimate the potential % germination of an unknown test lot of peanut seed using the leachate seed quality test. When the model is solved for % germination, as:

$$\% \text{germination} = (1.65 - \text{efflux rate})^{10.75}$$

and reprogrammed into the microcomputer the potential % germination may be predicted, automatically as a part of the leachate test.


ASYMPTOTIC MEAN SQUARE PREDICTION ERROR
FOR THE GENERAL MULTIPLICATIVE SEASONAL ARIMA MODEL
WITH ESTIMATED COEFFICIENTS.

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Abstract. It is well known in the literature on econometric model forecasting that the variance of the forecast error distribution should account for forecast errors arising from at least three sources. They are: 1) errors arising from the effect of unforeseen shocks to the system in the period between the time the forecast is computed and the forecast horizon; 2) those arising from the effect of parameter estimation from a finite sample; and 3) those arising from the effect of exogenous variable forecast errors. The literature on forecasting from Autoregressive Moving Average Models is less well formulated. Box and Jenkins point out that the problem of finding a manageable expression for the variance of forecast error when predicting more than one step ahead from an ARIMA model with estimated coefficients is difficult except for the simplest first order models. Their recommendation is to ignore the effects of parameter estimation on forecast error and compute the second moment of the forecast error distribution as if the coefficients are known with probability one. Later research has attempted to improve and generalize these results. Asymptotic mean square prediction error calculations which do take account of the effect of parameter estimation have been derived for the general ARMA(p,q) model when forecasting h steps ahead. In this paper, we will be concerned with the derivation of the first two moments of the forecast error distribution when the forecasts have been generated h steps ahead from the general multiplicative seasonal ARIMA model of order (p,d,q) x (P,D,Q)s whose coefficients have been estimated. A numerical example will also be presented and will be compared with numerical estimates of forecast error variance generated from calculations which fail to take account of parameter estimation.
A mathematical model will be developed to simulate the occurrence of flight activity by sharpnosed leafhoppers, *Scaphytopius magdalensis*, in blueberries. Incorporated in the model, will be the abiotic factor(s) responsible for initiating and suppressing leafhopper movement during the adult stage of each generation. Information from the simulations may be useful in improving the timing of current control strategies in blueberry IPM programs.

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Information on the regional patterns of southern pine beetle infestation dynamics were analyzed through the complementary statistical techniques of principal components and space-time autocorrelation analysis. The two approaches yield results of interest to modelers of the system. Specifically, the system exhibits a strong regional coordination during epidemics, few modes of subregional behavior, a strong trend in time, and a short spatial connection structure. The notion of source areas is discussed as it relates to these findings.

A Stochastic Simulation Model for Large Scale Southern Pine Beetle (*Dendroctonus frontalis* Zimmermann) Infestation Dynamics in the Southeastern United States.

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A simple multiple linear regression approach was taken towards modeling the yearly patterns of infestation by southern pine beetle in the southeastern United States. Each area's activity is predicted by a linear equation using three temporal lag values from the immediate locale and one spatial lag value from the surrounding areas. The fit of each equation is tested by examining its error structure in both an isolated and an integrated position. The addition of randomly generated error terms and of boundary conditions of area intensity values leads to a full stochastic simulation model for the system. This simulation model is then tested by a series of nonstandard tests for its adequacy as a proper model for the observed system. The usefulness, implications, and limitations of this model are then discussed.
Spring emergence of plum curculio and many other coleopteran pests is the result of two discrete processes—diapause termination and post-diapause migration. Photoperiod and temperature have been examined as predictors of diapause termination in the field using degree day models. The effects of temperature and humidity on spring migration are being analyzed using controlled humidity and temperature chambers and probit techniques. Field tests will explore the effect of micro-climate on spring emergence phenomena.
Costs of handling and loss of functional properties of frozen liquid whole egg (LWE) has stimulated interest in a refrigerated product. To maintain adequate shelf life at refrigeration temperatures a heat treatment more severe than normal pasteurization may be needed. To establish limits for the thermal treatment and to prevent possible damage to the pasteurization system due to coagulation of the product, flow properties of LWE during pasteurization were investigated. Utilizing a cone and plate viscometer, egg viscosity was determined at shear rates between 1.15 and 450 sec\(^{-1}\). Test temperatures varied from 20 to 75°C and heat treatment durations ranged from 0.5 to 10 min. Percent protein denaturation for each treatment was also determined and correlated to the flow properties. Above 60°C viscosities were shear rate dependent while below this temperature flow properties were approximately Newtonian. Mathematical expressions were developed for viscosity as a function of time, temperature and shear rate.
EFFECT OF ULTRA HIGH TEMPERATURE PROCESSING AND STORAGE CONDITIONS ON RATES OF SEDIMENTATION AND FAT SEPARATION OF ASEPTICALLY PACKAGED MILK

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Journal of Food Science (In press)

Rates of sedimentation and fat separation were determined for stored UHT treated milk. For each of three thermal treatments used for indirect and direct heating, homogenization pressures were 0, 10.34 or 20.68 MPa. Storage temperatures were 7, 22 and 35°C. Initial sediment deposits were greater for the direct system. Sedimentation increased with increased heat treatment and/or storage temperature but decreased as homogenization pressure increased. The indirect system had higher activation energies for sedimentation for all homogenization pressures. Fat separation rates tended to increase with increased storage temperature. The direct system tended to produce more sediment and less fat separation than the indirect system for a given thermal treatment.
LIPID OXIDATION DETECTION BY FOURIER ANALYSIS OF GAS CHROMATOGRAPHIC PROFILES

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Fourier coefficients computed from headspace gas chromatographic profiles of stripped corn oil samples can be used to estimate the degree of lipid oxidation and stability in these samples. It is shown that as few as 50 coefficients from the fourier domain can be used in a stepwise multiple regression model to accurately predict the oxidative state as measured by both peroxide and 2-thiobarbituric acid concentrations.
Product constituent losses in ultra high temperature processing were examined with Arrhenius kinetics. An iteration procedure was utilized to develop time-temperature relationships for tubular heating systems. After introduction of the time-temperature relationship into the Arrhenius equation integration was performed to yield relationships representing product constituent losses. Time-temperature conditions for a direct system required to achieve the same losses were determined. A unique condition developed where direct and indirect systems may be designed having equivalent losses, independent of activation energies. An example is demonstrated utilizing whole milk heated by commercially available direct for fifteen different indirect heating conditions. The mathematical uniqueness of the equivalence is examined.
A METHOD FOR PREDICTING GELATION OF
ASEPTICALLY PACKAGED STEAM INJECTED UHT MILK

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Journal of Food Science 48:1376-1377, 1983

The gelation of sterile UHT steam injected dairy products was investigated
by determining the time of gelation onset and the gelation rate. Fat percentages
of the products were 0.5, 3.25, and 10.5. Each product was processed at 411 °K
for 20.3 s, 416 °K for 6.9 and 20.3 s, and 422 °K for 3.4, 6.9, and 20.3 s. Products
were stored at 277 and 297 °K. Viscosity measurements were taken with four
commercial viscometer assemblies and viscosity data compiled at a shear rate of
1 s⁻¹. Velocity rate constants (k) were determined using regression analysis.
Prediction equations were formulated for the time of gelation onset and the rate
of gelation depending on the severity of the thermal treatment, percent fat and
storage temperature.
The effect of milk fouling deposits on the heat transfer rate of a tubular heat exchanger was investigated for varying process heat treatments. Product input and discharge temperatures were maintained constant while steam temperature increased as deposits formed. Processing conditions included product entrance temperatures of 347.6 and 366.4 °K for heater exit temperature of 410.7 °K and product velocity of 1.58 m/s; 363.9 and 366.7 for 410.7 and 2.70; 364.6 for 410.7 and 3.25; 370.6 and 357.8 for 427.4 and 1.58; 378.5 for 427.4 and 2.70; and 379.5 and 376.3 for 427.4 and 3.25. Predictive expressions representing product deposition were determined for process variables, heating curve variables, and equivalent times and temperatures representing the thermal treatment. Product constituent losses during the fouling process and aspects of fouling kinetics were examined.
The gelation of UHT steam injected dairy products was investigated by determining rheological model constants. Fat percentages of the products were 0.5, 3.25 and 10.5. Each product was processed at 143°C for 6.9 s and stored at 24°C. At four week intervals, from 55 to 85 weeks storage, cone and plate creep-relaxation data was collected. Three element rheological models were developed for each test date. Empirical relationships were derived relating the elastic and viscous constants to storage time for each fat content. The strongest parameter for all samples was the series elastic constant. The viscous constant was next with the Kelvin elastic constant being much weaker. All constants for all samples increased over storage time as gelling progressed (apparent viscosity increased). The lower the percent fat, the sooner gelling started and the faster the rate. The gelation of UHT milk was examined and found to depend heavily on the percent fat.
A Growth and Yield Model for Natural Stands of Piedmont and Red River Bottomland Hardwoods

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Models to project basal area and tree survival from site index, initial age, basal area, trees per acre, and stand dominant height are developed for natural stands of Piedmont and red river bottomland hardwoods. The Richards generalization of the von Bertalanffy growth equation is fit using remeasurement data from permanent plots in evenaged stands located across the Southeast. Parameter estimates for the nonlinear models are obtained using a computer-aided iterative search procedure. The parameters for both models are defined using measured stand variables. Acceptable results are obtained when the equations are applied to data sets not used in the original model development. The final equations represent biologically reliable projection models for basal area and surviving trees per acre.
Simple mathematical models were developed to relate environmental parameters to habitat quality for a selected number of bird and mammal species on Croatan National Forest. Field data were collected at systematically distributed sample points, and maps of environmental parameters were developed using a cellular, computer-mapping program (SYMAP). These data were used as input in the species-habitat models, and the spatial distribution of habitat quality was mapped. This map was then compared with the distribution of animal population density to test model performance.
GROWTH ESTIMATION
OF MIXED SOUTHERN HARDWOOD STANDS

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Southern hardwood stand growth on seven forest site types was determined through remeasurements on a series of permanent sample plots stratified by age. Growth, as a predicted change in merchantable basal area and as a predicted change in the dominant tree height of the stands, is related to the ratios of yields at 5-year intervals for various yield parameters. The use of these ratios allows the growth prediction to be applied to any forest-tree yield table or equation.
Joint Analysis of Genotypic and Environmental Effects

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A definition of jointly contributing genotypic and environmental effects is introduced, from which a new concept of GE interactions is derived. Interaction is defined to be the failure of genotypic or environmental response functions to be separable.

For separable response functions, the contributions of the genotypic and environmental effects must be related in terms of an operator which can describe their joint actions. A scale-free method of determining the simplest operator is developed in terms of comparative norms of reaction and a characteristic of the operator is given for several operators. With a defined operator, the genetic and environmental contributions can be derived, and biologically interpreted.

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Conditions for Protected Polymorphism
in Subdivided Plant Populations
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Pollen and seed migration patterns are not the same in most plant populations, and the differences affect conditions for protection of alleles. We analyzed conditions for protectedness when pollen is freely exchanged among all demes, while seeds are deposited within the female parents' deme. Protectedness was analyzed at the boundary of fixation and necessary conditions were derived.

If no selection among female genotypes exists, then simple average heterozygote superiority in the males can guarantee protection. However, regardless of the form of selection in females, simply doubling the male heterozygote superiority can still guarantee protectedness. Conditions for guaranteeing protectedness with female selection were also derived but are more complicated.

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Conditions for Protected Polymorphisms

In Subdivided Plant Populations: 2. Seed Vs. Pollen Migration

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The effect of sex-dependent migration and selection are explored within the general context of Wright's island model of migration. An analysis for the development of protection of polymorphisms is constructed for a migratory system in which pollination is strictly localized within mating-selection demes, but fertilized seed from each deme create a zygotic pool for regenerating all demes. It is found that selective differences in pollen and ovule production affect the maintenance of polymorphisms in different ways and that a mixture of homozygote excesses and deficiencies can exist for different alleles at a multi-allelic locus.

A system of sedentary pollen with migrating seed is contrasted with a system of migrating pollen with sedentary seed distribution. This latter system is strongly protective of polymorphisms and always creates a deficiency of homozygotes below Hardy-Weinberg expectations even in the absence of selective differences. The effect of the sexes on evolutionary dynamics is not just a matter of reversing sex roles since gamete versus zygote dispersal requires different supporting effects from the migrating and sedentary sexes.

Finally, these two systems are compared with systems of pollen and seed migration and with pollen and seed localization with respect to the protection afforded polymorphisms and departures of homozygote frequencies from Hardy-Weinberg expectations. The effects of environmental heterogeneity on all systems are also compared. Relationships of these models to other models are drawn.

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FREQUENCY-DEPENDENT SELECTION IN LOGISTIC GROWTH MODELS

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This paper studies the dynamics of mathematical models of a continuously reproducing diploid population with two alleles at one locus. The dependent variables are allele frequency and population density. We modify the basic density dependent logistic growth model by inserting three possible types of frequency dependence in the fitness functions. These models are analyzed and contrasted with the purely density dependent situation. Examples are given having periodic fluctuations in allele frequency and population density, which is impossible for purely density dependent fitness functions.
A MODEL FOR CANNIBALISM

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This project concerns the mathematical behavior and biological implications of a proposed deterministic model for cannibalism in a species whose life cycle consists of a sequence of distinct stages, and in which members of later stages feed on those in earlier stages. The model consists of a system of differential equations which, under certain conditions on the birth and death parameters, has a unique equilibrium point at which all stages contain some members. Questions of stability and limiting behavior are under investigation.
A mathematical model using a Leslie matrix approach was developed to estimate survivorship, natality, and rate of increase for a "snap shot" sample of the age distribution of a bobcat population. The method relaxes the assumption of an age distribution that is currently stable by assuming such a distribution occurred sometime in the past. Results of the estimates using this approach were comparable to estimates of these parameters using 2 separate yearly samples in a standard Leslie matrix analysis.
A family organization in which only the adults breed establishes an upper limit to the size of beaver (Castor canadensis) family units (colonies). The value of the limit is determined by natality, mortality, and dispersal rates that may vary as functions of population density or other factors. We develop a mathematical model to describe the complex interplay among natality, mortality, and dispersal and to estimate dispersal rates of subadults from natal colonies. The model leads to an equation which is used to predict average colony size for established colonies. Figures illustrate predictions of colony size for various combinations of survivorship, dispersal and other parameters.
A STOCHASTIC MODEL OF BEAVER POPULATION GROWTH

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pp. 1215-1245 in J. A. Chapmanard and D. Pursely, Eds.
Worldwide Furbearer Conference. 3 Vols. 2056 pp.

A mathematical model of the growth phase of an unexploited beaver (Castor canadensis) population was developed based on field observations of the life history of beaver colonies and was compared with empirical observations of population growth in Massachusetts. Dispersal rates of subadults from their natal colonies were considered to be density dependent; i.e., as population density increased the rate of dispersal decreased. The rate of pair formation between dispersed individuals was varied as a function of the number of occupied colony sites within an area containing a fixed number of suitable sites.

The dynamics of natality, mortality, and dispersal were considered as flows between appropriate age classes; i.e., kits, yearlings, subadults, adults in newly established colonies, and adults in previously established colonies. The model described population growth as a system seeking homeostasis. Effects of colony site degradation were not considered.

A stochastic simulation computer program based on the model is explained and simulation results are given. By equating the number of breeding females to the number of established colonies, estimates of mean colony size and age composition are derived. The simulation results provided insight into the size of a "floating population" of dispersed subadults and the magnitude of rates of successful colony establishment.
Reaction-Diffusion Equations with Nonlinear Boundary Conditions

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This paper is concerned with some enzyme reaction problem where two types of enzyme concentrations are governed by a coupled system of reaction-diffusion equations. A novelty of this system is that the coupling effect is through the boundary condition by a nonlinear relationship between the two concentrations. This includes the cases of mutual inhibition and mutual activation as well as the case of activation-inhibition. Some mathematical results on the existence-uniqueness question of the coupled partial differential equations and the asymptotic behavior of the solution are given.
Asymptotic Behavior of a Reaction-Diffusion System in Bacteriology

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In the study of pattern formation by bacteria, Hoppensteadt and Jüger proposed a mathematical model which describes the histidine concentration $u$, the buffer concentration $v$, and the bacterial population density $w$. Their model involves a coupled system of reaction-diffusion equations in the form

$$
\begin{align*}
    u_t - D_1 \nabla^2 u &= -awf(u,v), \\
    v_t - D_2 \nabla^2 v &= -bwf(u,v), \\
    w_t &= cwf(u,v), \quad (t > 0, x \in \Omega)
\end{align*}
$$

where $\Omega$ is a bounded domain in $\mathbb{R}^2$, $\nabla^2$ is the Laplacian operator in $\Omega$, $D_1, D_2, a, b, c$ are positive constants, and $f$ represents the rate of growth competence. In the above balance equation, $af$ represents the uptake rate of histidine, $bf$ the acid production by growing cells, and $cf$ the bacterial growth rate. Based on the Michaelis-Menton hypothesis, the function $f$ is given by $(u/(u + k_1))(v/(v + k_2))$. Under the basic boundary condition of Neumann type or mixed type, the coupled system may have infinitely many steady-state solutions. The purpose of this paper is to give a method for the construction of the solution and some explicit information on the asymptotic limit of the time-dependent solution in relation to these steady-states.

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Asymptotic Behavior of a Competition-Diffusion System
in Population Dynamics

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J. of Nonlinear Analysis TMA, 6: 1163-1184, 1982

This paper continues the discussion of the coexistence problem between
two competing species in a bounded habitat where the spatial effect of
dispersion is taken into consideration. This leads to a coupled system of
Lotko-Volterra type reaction-diffusion equations. Both the time dependent
and the steady-state problems are considered. In most cases the steady­
state problem has more than one solution and the number of solutions may
be affected by the boundary condition. One of the problems investigated
in this paper is to identify the stable steady-state solution(s) from which
one can determine whether the competing species coexist or one wipes out
the other. When the system has two or more steady-state solutions a
detailed analysis on the stability region for each of the steady-states
is given. Another question discussed in the paper is the case when one
species dominates the other. By a suitable choice of a harvesting function
the dominating species can be controled so that the two competing species
become coexisting.
DYNAMICAL BEHAVIOR OF DIFFERENTIAL EQUATION MODELS OF FREQUENCY AND DENSITY DEPENDENT POPULATIONS

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Journal of Mathematical Biology (in press)

This paper studies the dynamics of a mathematical model of a continuously reproducing diploid population with two alleles at one locus. The dependent variables are allele frequency and population density. If the genotype fitnesses are frequency and density dependent, the stability of equilibria is related to the geometry of the zero allele fitness curves. The asymptotic behavior of solutions where fitness is only density dependent is contrasted to the asymptotic behavior where fitness is frequency and density dependent. A parameterized family of fitness functions giving a Hopf bifurcation and limit cycles is investigated analytically and numerically.
ADVANCEMENTS IN THE DEVELOPMENT
OF A PEANUT LEAFSPOT FORECASTER

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A second generation peanut leafspot forecaster will be tested in the 1983 growing season. This battery operated, electronic weather station gathers temperature and relative humidity readings hourly and issues a spray advisory each 24 hours. 'Favorable' (spray) or 'not favorable' (do not spray) advisories are based on the previously defined relationship between the number of hours of high humidity (≥ 95%) and the temperature during that humidity period (Plant Dis. Reprtr. 50:810-814, Phytopathology 64:385-388). Changes from the original model include: using the average rather than minimum temperature during the high humidity period and using the hours of 95% RH and leaf wetness rather than just the hours ≥ 95% RH. The forecaster is equipped with an 8K RAM if weather data storage is desired. This data can be retrieved via a 4 digit LCD display or through an RS-232 port for interfacing with larger computers. A built-in modem will allow remote weather data or forecast interrogation. Synthetic speech will also be added for direct telephone access of forecasts by humans. A new type of relative humidity sensor based on thermal electric cooling of a leaf wetness meter will be utilized. Any disease models which utilize temperature, humidity, leaf wetness or rainfall (port is available for rainfall gauge) can be programmed into this forecaster by burning a ROM chip.
Modeling Genetic Interactions Between Populations of Plants and Their Parasites

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Many important diseases of plants are caused by parasitic fungi for which there is a gene-for-gene relationship between resistance in the host species and virulence in the parasite. Plants without specific resistance genes are susceptible to even those parasite genotypes that lack specific virulence genes, but plants with specific resistance genes can be attacked only by parasites with matching virulence genes. In coevolving host-parasite systems, alleles for resistance and susceptibility in the host and for virulence and avirulence in the parasite appear to occur together at many loci in more or less balanced polymorphisms. Theoretical models of such systems may lead to better understanding of their stability and suggest improved strategies for using resistance genes to provide durable protection from disease in agricultural crops.

References


Recent literature in apple tree bud physiology in dormant period is reviewed. Special attention is given to environmental and endogenous factors controlling dormancy as well as mechanism of control and nature of dormant states. Further work needed for developing a model of bud dormancy in relation to temperature and other environmental factors is discussed.
MEASURING GENETIC VARIABILITY IN PLANT POPULATIONS

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In Isozymes in Plant Breeding and Genetics, Editors  

In this chapter, we first recall the properties of isozyme technology which lend themselves to estimating genetic variation, and mention the technical pitfalls which can occur. Then follows a survey of the important measures of variation and its structure, with their estimators and sampling variances in particular cases. Decisions on optimal sampling strategy are discussed. In general, research on and rigorous formulation of this statistical methodology is incomplete, but improvements in this area are likely to appear in the coming years. Finally, we consider some uses that have been made of estimates of variation.
PARAMETER ESTIMATION FOR STOCHASTIC DIFFERENTIAL EQUATIONS
BY INDEPENDENT-INCREMENT NOISE

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Suppose that it is desired to estimate the parameters of the stochastic differential equation \( dx_t = \gamma(x_t)dt + \sigma(x_t)dn_t \), where \( \sigma(x) \) is a known function and \( n_t \) is a stochastic process with stationary independent increments and known infinitesimal moments \( n_k \). For example, \( n_t \) could be mixed Poisson and Weiner noise. We give a new estimator for the unknown parameters of \( \lambda(x) \) that does not require Ito stochastic integration. The new estimator compares favorably with previously developed estimators, such as the Kailath estimator. Examples based on computer simulations are given.
Several variations of a method for detecting linkage between a marker locus and a quantitative trait in full sib families are presented along with computational details. All variations are based on contrasts within qualifying families of three or more sibs. The empirical powers of the various test statistics, evaluated by simulation, were very similar, and also similar to that of Smith. These single-generation tests are likely to be successful only for many families and relatively tight linkage.
The variances of actual inbreeding and coancestry in terms of their corresponding identities by descent were studied for finite populations. For inbreeding at a single locus, the total variance \( \sigma^2 = F(1-F) \) (\( F \) is the inbreeding coefficient) is comprised of a component \( \sigma^2_w \) within populations and a component \( \sigma^2_b \) between replicate populations. These variances increase in time to a maximum at about \( 1.1N_e \) generations for \( \sigma^2_w \), about \( 2.3N_e \) generations for \( \sigma^2_b \), and about \( 1.4N_e \) generations for \( \sigma^2 \), and decrease thereafter (\( N_e \) is effective population size). The ratio \( \sigma^2_b/\sigma^2 \) is ever increasing to an asymptote in the range 0.4-0.5 depending on \( N_e \) and the mating system. For finite populations with variation in pedigree F's, there are contributions \( \sigma^2_{wF} \) within and \( \sigma^2_{bF} \) between populations. The component \( \sigma^2_{bF} \) is insignificant except for very small populations, and \( \sigma^2_{wF} \) is largest in the early generations and then decreases roughly as \( (1-F)^2/KN_e \) where \( K \) is formulated in terms of the mating strategy and the degree of avoidance of mating relatives. An additional degree of avoidance increases \( K \) by a factor of 4. In a large population at equilibrium with respect to mixed self and random mating, \( \sigma^2_{wF} \) accounts for one-half to two-thirds of \( \sigma^2_w \). Bringing in more loci leads to the decomposition of the total variance into four components whose values are affected by linkages among the loci. The relationships between these components and \( \sigma^2_w, \sigma^2_b, \sigma^2_{WF}, \) and \( \sigma^2_{bF} \) are elaborated in terms of tight and loose linkage. The exact computations of \( \sigma^2_{WF} \) and \( \sigma^2_{bF} \) require the use of two-locus descent measures without linkage. The variances of various averages of actual identities by descent, such as the proportions for individuals or populations, are formulated for a sample of individuals.
Covariances of all parent and first generation relatives from outcrossing or self-fertilization from a parent population, which is in equilibrium with respect to self-fertilization and outcrossing, are considered. The results are for any number of alleles and loci with additive and dominance effects and are phrased in terms of six quadratic genetic components whose coefficients are given by descent measures for equilibrium populations. The expressions include joint contributions of loci to the variances and covariances of relatives because of the variation in the inbreeding coefficients for this system of mating. By inclusion of the full complement of relatives, all quadratic components can be estimated. The findings of Ghai (1982) for compound functions of the covariances with two alleles at a single locus are analyzed in terms of the more general model.
Application of Maximum Entropy and Minimum Cross-Entropy Formalisms to Stochastic Modeling of Complex Dynamic Systems; Formulation of the Problem.

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The general problem addressed is that of using data and observations to infer a probability distribution on the state space of a system and of making inferences concerning the time dynamics of that probability distribution. The goal is to make full use of the available information but without imputation of "information" which we do not in fact have. The approach is through extension of the information theoretic methods of maximum entropy and minimum cross-entropy. Problems which must be addressed are formulated and an approach is suggested which rests on introduction of additional relationships drawn from theory of dynamic system modeling. The methodology is intended as a tool in the stochastic modeling of biological systems, with special emphasis on application to ecology and environmental management.

A Survey of Decision Modeling Formalism As Applied to Pest Management.

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Biomathematics Series No. 15, Institute of Statistics Mimeo #1634, NCSU, 1983.

A survey of types of decision models with respect to their use for insect and disease control in agriculture. The term decision model is taken to include any formal modeling structure designed to aid in decision making, and includes the models of a mathematical programming, optimal control, dynamic programming and stochastic control. These are discussed within the conceptual framework of applied decision analysis. The emphasis is on the relative potential of various approaches to pest control modeling, and the extent to which that potential has been exploited.
Models for chemical control of plant disease must include the disease epidemiology, dynamics of pesticide application, redistribution and decay, and the effects of pesticide on the disease organism. The discussion reviews the epidemiology of sooty blotch and flyspeck diseases of apple, the mechanism of fungicidal control with special reference to use of captan and zineb, and the dynamics of fungicide residue deposit on decay. The discussion focuses on identification of the principle relationships which must be included in the formulation of a mathematical model.

The starting point for this work is the premise that low levels of southern pine beetle are endemic to the forest system, so that the work focuses on the transition between the endemic and epidemic regimes. A preliminary problem is the definition of the concept of "epidemic".

The endemic to epidemic transition is dependent upon the relatively rare (low probability) passing of a threshold, whose value is itself a random variable. The system is examined in a hierarchy of levels: the individual tree level, neighborhood level, locality of connected or contiguous stands, level of large geographical region. The concepts of threshold and of the endemic/epidemic transition have a specific interpretation at each level.
System Analysis and Modeling in Extrapolation of Controlled Environment Studies to Field Conditions

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Department of Soil Science


Focuses on the role of mathematical system modeling in helping to interpret results of controlled environmental studies for evaluating effects of stress conditions on crop growth. Emphasis is at the broad conceptual level, rather than at the level of specific case studies.

A Modeling Strategy for the Orchard Ecosystem

Department of Statistics, Biomathematics Division


Formal models are treated as a means for efficient use of available information, as means for identifying potential useful new information, and of efficiently gathering new information. A "horticentric" viewpoint is adopted in which components of the system enter the model only in terms of their direct or indirect effects on fruit production. Specific strategies are discussed for modeling dynamics of fruit production, effects of pest interactions, and for interfacing the biological model with economics.

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THE RELATION BETWEEN DISCHARGE REGULARITY AND RESPONSES TO EXTERNALLY APPLIED GALVANIC CURRENTS IN VESTIBULAR-NERVE AFFERENTS OF THE SQUIRREL MONKEY

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Most vestibular-nerve afferents can be classified as regularly or irregularly discharging. Two factors are theoretically identified as being potentially responsible for differences in discharge regularity. The first, ascribable to synaptic noise, is the variance ($\sigma_v^2$) characterizing the transmembrane voltage fluctuations of the axon's spike-trigger site, i.e., the place where impulses normally arise. The second factor is the slope ($d_u^v/dt$) of the trigger site's postspike recovery function. Were ($d_u^v/dt$) a major determinant of discharge regularity, the theory predicts that the more irregular the discharge of a unit, the greater should be its sensitivity to externally applied galvanic currents and the faster should be the postspike recovery of its electrical excitability. The predictions would not hold if differences in the discharge regularity between units largely reflected variations in $\sigma_v^v$.

To test these predictions, the responses of vestibular-nerve afferents to externally applied galvanic currents were studied in the barbiturate-anesthetized squirrel monkey. Current steps of 5-s duration and short (50 $\mu$s) shocks were delivered by way of the perilymphatic space of the vestibule. Results were similar regardless of which end organ an afferent innervated. The regularity of discharge of each unit was expressed by a normalized coefficient of variation (cv*).

The galvanic sensitivity ($\beta_p$) of a unit, measured from its response to current steps, was linearly related to discharge regularity (cv*), there being approximately 20-fold variations in both variables across
the afferent population. Various geometric factors—including fiber diameter, position of individual axons within the various nerve branches, and the configuration of unmyelinated processes within the sensory epithelium—are unlikely to have made a major contribution to the positive relation between $\beta$ and $cv^*$. The postspike recovery of electrical excitability was measured as response thresholds to shocks, synchronized to follow naturally occurring impulses at several different delays. Recovery in irregular units was more rapid than in regular units.

Evidence is presented that externally applied currents acted at the spike-trigger site, rather than elsewhere in the sensory transduction process.

An afterhyperpolarization model simulates many features of the steady-state discharge of vestibular afferents, provided that firing rates are higher than 40 spikes/s. To explain the linear relation between $\beta_p$ and $cv^*$ requires that units differ in both their synaptic noise ($\sigma_v$) and the slopes of their recovery functions ($du_v/dt$). The more irregular the discharge of a unit, the greater is its $\sigma_v$ and the smaller its $(du_v/dt)$. Of the two factors, $(du_v/dt)$ is estimated to be nearly four times more influential in determining variations in discharge regularity across the afferent population.

We argue that the irregular discharge of some vestibular afferents offers no functional advantage in the encoding and transmission of sensory information. Rather, the irregularity of discharge is better viewed as a consequence of the enhanced sensitivity of these units to depolarizing influences, including afferent and efferent synaptic inputs.
A MATHEMATICAL MODEL FOR THE JOINT METABOLISM OF NITROGEN AND ENERGY IN CATTLE†

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SUMMARY

A mathematical model for the joint metabolism of nitrogen and energy has been developed and its utility studied. It takes into account digestion, absorption, anabolism, catabolism, and excretion of nitrogenous and non-nitrogenous nutrients. The model consists of a set of non-linear differential equations which, upon integration, yield predictions for changes in body proper and energy stores and for outputs of milk, heat, methane, and nitrogenous and non-nitrogenous wastes. Key aspects are the modes whereby nitrogenous and non-nitrogenous nutrients combine for body growth and milk production and nitrogenous nutrients split into non-nitrogenous nutrients and nitrogenous wastes.

Values for some of the model parameters were obtained from the literature, but many of the important ones had to be estimated from experimental data. Estimation was accomplished by iterative weighted least squares fitting of the model to published results from energy and nitrogen metabolism trials on growing steers and on milking and non-milking cows fed widely-varying protein and energy intakes.

The model was tested with metabolism data from trials not used in estimating parameters. Over 70%, of the comparisons for daily output of faecal nitrogen and energy, urine nitrogen and energy, milk nitrogen and energy, and methane showed deviations between prediction and observation of 20%, or less. These deviations were little greater than the discrepancy between observations for replicate trials, thus establishing a basic soundness of the model.

Although fitted and tested with cattle, the model applies in principle to animals generally and man, for predicting outputs from widely-varying nitrogen and energy inputs as conditioned by species, type and physiological state. The model, with some extension, should permit more profitable ration formulation than do extant approaches over a very broad domain of feeding and price situations.

† This work was supported by Public Health Service Grant No. GM-678 of the National Institute of General Medical Sciences.
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ESTIMATION METHODOLOGY IN CONTEMPORARY SMALL MAMMAL CAPTURE-RECAPTURE STUDIES

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J. Mamm., 64(2):253-260, 1983

Estimators of population size and survival rate based on the Jolly-Seber capture-recapture model and the "enumeration method" are described. Enumeration estimators are shown to estimate complicated functions of capture and survival probabilities and, in the case of the population size estimator, population size. Frequently-listed reasons for preferring enumeration estimators are discussed and the Jolly-Seber estimators are shown to be superior even in the case of heterogeneity and trap-happy response, the two sources of unequal capture probability most likely to occur in small mammal studies. New developments in probabilistic capture-recapture models are described, and these models are recommended for future small mammal capture-recapture studies.
Methods currently used to estimate taxonomic extinction probabilities from fossil data generally assume that the probability of encountering a specimen in a particular stratum, given that the taxon was extant in the time period and location represented by the stratum, either equals one or else is a constant for all strata. Methods used to estimate taxonomic diversity (number of taxa) and speciation rate generally assume that encounter probabilities equal one. We suspect that these assumptions are often false. Capture-recapture models were historically developed for estimation in the face of variable and unknown sampling probabilities. These models can thus be used to estimate parameters of interest from paleobiological data when encounter probabilities are unknown and variable over time. These models also permit estimation of sampling variances, and goodness-of-fit tests are available for assessing the fit of data to most models. Here, we describe capture-recapture models that should be useful in paleobiological analyses and discuss underlying assumptions. We illustrate these models with examples and discuss aspects of study design. We conclude that these models should prove useful in paleobiological analyses.
CAPTURE-RECAPTURE MODELS ALLOWING FOR AGE-DEPENDENT SURVIVAL AND CAPTURE RATES

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Biometrics 37, 521-529, September 1981

A K-sample capture-recapture model for an open population of animals, which allows for different identifiable age categories to have different survival and capture probabilities, is developed. Explicit maximum likelihood estimators of population size and survival rates, together with their asymptotic variances and covariances, are given. A test of whether survival and capture rates are independent of age is shown to be of simple hypergeometric form. An illustrative example based on resighting data of neck-collared giant Canada geese (Branta canadensis maxima) is presented. The relationship of this model to other capture-recapture and band-recovery models is discussed.
THE USE OF AN AGE-DEPENDENT MARK-RECAPTURE MODEL IN FISHERIES RESEARCH

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An age-dependent generalization of the Jolly-Seber mark-recapture model for fish populations subject to birth, death and migration is illustrated using data from a study on pike (Esox lucius) in Dorset, England. These data show strong evidence of differential survival with age. We estimate the average annual survival rate to be 50% for the pike aged two or more years and 34% for those of age one year.

We believe that this age-dependent mark-recapture model could be very useful for a wide range of fisheries research and management problems. Often in fisheries work the assumption that survival is independent of age has not been examined critically.

We present guidelines helpful in designing mark-recapture studies. This includes a useful design which increases precision, and also allows population size estimation to be robust to unequal catchability (heterogeneity or trap response) within an age class.

The mark-recapture method is widely used in fisheries biology to estimate population numbers, survival rates, and recruitment rates (Cucin and Regier 1966, Ricker 1975, Arnason and Mills 1981). The Jolly-Seber model (Jolly 1965; Seber 1965) is a stochastic (or probabilistic) mark-recapture model for an open population of animals. (By open we mean that the population could be subject to birth, death and migration processes during the mark-recapture experiment.) This model depends on the assumption that the probabilities of survival and capture are independent of the age of the animal. For an excellent technical description see Seber (1973; p. 196). An intuitive discussion for biologists is given in Pollock (1981a).

Pollock (1981b) developed a model which allows identifiable age-classes to have different survival and capture probabilities. Here the age-dependent model is reviewed and then extensively illustrated using a data set on pike (Esox lucius) collected from a section of the Frome River in Dorset, England (Mann 1980). We also present some guidelines on designing mark-recapture studies and a discussion of the utility of the age-dependent model in fisheries research and management problems.
ASSUMPTIONS OF MODERN BAND-RECOVERY MODELS, WITH EMPHASIS ON HETEROGENEOUS SURVIVAL RATES

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J. Wildl. Manage. 46(1):88-98, 1982

The assumptions inherent in modern band-recovery models are reviewed with particular attention to homogeneity of survival and band recovery rates for all individuals in the population. If this assumption fails, the following implications emerge: (1) the models only enable estimation of average annual survival and band-recovery rates; (2) estimators of these averages probably give underestimates; (3) the degree of underestimation in practical studies is difficult to assess, but may sometimes be important for survival estimates; (4) if sampling is nonrandom and heterogeneity of survival and recovery rates is present in the population, then any estimates could be misleading; and (5) if survival rates are homogeneous but recovery rates are heterogeneous (due perhaps to geographical variation in hunting pressure and reporting rates), then there is no bias in survival estimates. An example where data from neck-collared birds showed heterogeneity in segments of a Canada goose (Branta canadensis) population is discussed. We believe that the practical limitations of bird-banding studies deserve careful review by population biologists and managers.
ON THE DETECTION OF CLUSTERING AND ANISOTROPY USING BINARY DATA FROM A LATTICE PATCH

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ABSTRACT

A method is suggested for detecting spatial pattern of disease data on a rectangular lattice. One first classifies all pairs of points by their distance and orientation of separation and then counts the number of pairs of points in each distance-orientation type for which both points show the disease. A log-linear model is proposed for these counts. Methods of fitting to it are suggested that furnish tests of clustering and of anisotropy. Empirical sampling results show that the tests are reasonably powerful against certain alternatives and verify that nominal levels of significance are approximately correct. The method is given in detail for a single four by five plot and is then adapted for combining data from many such plots. Examples are given of such counts and of the calculations used to analyze them.

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ESTIMATION OF THE COANCESTRY COEFFICIENT:  
BASIS FOR A SHORT-TERM GENETIC DISTANCE

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Genetics (in press)

A distance measure for populations diverging by drift only is based on the coancestry coefficient $\theta$, and three estimators of the distance $\mathcal{D} = -\ln(1-\theta)$ are constructed for multi-allelic, multi-locus data. Simulations of a monoecious population mating at random showed that a weighted ratio of single locus estimators performed better than an unweighted average or a least squares estimator. Jackknifing over loci provided satisfactory variance estimates of distance values. In the drift situation, Nei's distance $D$ has the disadvantages of depending on the unknown gene frequencies in the ancestral population, and of having a larger variance than $\mathcal{D}$ when there are many alleles at a locus.
A STOCHASTIC MODEL FOR THE EFFECTS OF INNERVATION PATTERN
ON DISCHARGE REGULARITY IN VESTIBULAR NERVES

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The firing patterns of mammalian vestibular nerve fibers differ in the regularity of their discharge. A theoretical consideration of the effects of innervation pattern, i.e., the spatial properties of the nerve's dendrites, on the firing patterns is presented. The thicker fibers are represented by an RC circuit model (Stein, 1965). The thinner fibers are represented as a semi-infinite RC cable with a sealed termination and with synaptic inputs spatially distributed over the 1st length constant from the sealed end. Each synaptic input site is assumed to produce a Poisson sequence of current impulses. Expressions for the steady-state moments of the resultant membrane potential are computed as a function of distance, along with the power spectral density. For a given mean voltage, the standard deviation over 1 to 2 length constants is quite insensitive to the spatial distribution of synaptic inputs. This result coupled with an approximation method for obtaining 1st passage times (interspike intervals) suggests that innervation pattern is not the major determinate of the discharge regularity differences seen in vestibular nerves. Further support for this suggestion is found in a recent experimental study (Goldberg, Fernandez, Smith, 1982), which implicates intrinsic sensitivity differences in the nerve's dendrite as the origin of regularity differences.
THE BROAD STREET PUMP REVISITED

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Inter. J. of Epidemiology 11(2):99-100, 1982

This historical note examines the effect of population migration of the number of fatal cholera cases reported by John Snow in the Golden Square area of London during the fall of 1854. A method to correct for population migration is given and its relevance to present day epidemiological studies discussed. The methodology can be extended to the problem of estimating the distribution of exposure by using one of several deconvolution techniques.
A PARADOX IN A RECENT MARKOV MODEL
FOR SYNAPTIC TRANSMISSION

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Stochastic differential equations (SDE's) have been widely used in neuronal modelling for the past 15 years (e.g. Stein, 1965). An apparent paradox that occurs in a recent nonlinear SDE model is presented, its source determined and a resolution proposed. Tuckwell (1979, J. Theor. Biol. 77:65-81) developed a model for the effects of synaptic transmission upon a neuron's trigger zone, which incorporated nonlinear summation of excitatory and inhibitory synaptic inputs (modelled as Poisson counting processes with positive and negative jumps respectively). While primarily concerned with the first passage time problem, Tuckwell also presented the Feller-Kolmogorov equation for the transition pdf and an expression for the mean as a function of time for the unrestricted process. Following his method, expressions for higher order moments can be obtained. However, a problem in the mean of the process becomes apparent in the limit of large arrival rates. The value of this limit is counterintuitive. The source of the problem lies in the boundary conditions. This model emphasizes the importance of boundary conditions in determining the qualitative behaviour of SDE models, as well as the care required in analyzing them.
Experimental studies on the growth of animal tumors have reported that, at least in some "average" sense, the tumors follow some saturating growth curve, usually the Gompertz growth curve. Earlier (Smith and Tuckwell, 1974) an explicit analytic expression for the probability density function of a stochastic Gompertzian growth process was obtained. The resultant random process was a nonlinear transformation of a Wiener process. Here we examine the estimation problem for this random process governed by the stochastic differential equation \( dx = x \log (K/x) \, dw(t) \), where \( K \) is the saturation level and \( w(t) \) is a non-zero mean Wiener process. The median, but not the mean, is found to reproduce the deterministic solution. Using the independent increment property, the mean and variance of the transformed data can be estimated by standard procedures. Rat adenocarcinoma data is used to illustrate the methods.
THE STATIONARY MOMENTS OF POISSON-DRIVEN
NON-LINEAR DYNAMICAL SYSTEMS

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Moment recursion relations have previously been derived for the
stationary probability density functions of continuous-time stochastic
systems with Wiener (white noise) input. These results are extended in
this paper to the case of Poisson (shot noise) input. The non-linear
dynamical systems are expressed, in general, as stochastic differential
equations, with an independent increment input. The transition
probability density function evolves according to the appropriate
Kolmogorov equation. Moments of the stationary density are obtained
from the Fourier transform of the stationary density. The moment
relations can be used to estimate the parameters of linear and non-linear
stochastic systems from empirical moments, given either Wiener or
Poisson input.
MEAN FIRST PASSAGE TIMES FOR THE CUSP CATASTROPHE DENSITY

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The cusp catastrophe density can be viewed as the steady state p.d.f. of a diffusion process on the real line with a cubic drift term and a constant diffusion coefficient. An expression for the mean first passage time (MFPT) is readily obtained using the method of Siegert (Phys. Rev. 81:617-623, 1951). The behaviour of the MFPT is examined as a function of the bifurcation and asymmetry parameters of the cusp density as well as the intensity of the diffusion term. In some cases, the passage time problem can be well approximated by a 2 state semi-Markov process. Finally, these results are compared with recent results on bistable potential wells in the statistical physics literature.
NONLINEAR DYNAMICAL SYSTEMS DRIVEN BY WHITE NOISE AND POISSON NOISE

Stationary moment recursion relations and drift estimators

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Moment recursion relationships have been derived previously for the stationary probability density of continuous time stochastic systems with Wiener (white noise) input, \( w(t) \), and with Poisson (shot noise) input, \( p(t) \). The case of simultaneous Wiener and Poisson inputs is examined here for the additive noise model

\[
dx(t) = - g(x) \, dt + dw(t) + dp(t),
\]

and the state dependent noise model

\[
dx(t) = - g(x) \, dt + x \left[ dw(t) + dp(t) \right],
\]

where \( g(x) \) is a finite order polynomial. The moment relationships are used to estimate the drift parameters of linear and nonlinear stochastic systems from empirical moments. The drift estimators, so derived, are shown to be consistent and asymptotically normal.
AN AFTERHYPERPOLARIZATION MODEL FOR VESTIBULAR AFFERENTS

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A stochastic afterhyperpolarization model, modified from Kernell [Brain Res. 11, 685-687 (1968)], simulates many features of the steady-state discharge of vestibular afferents, and may be relevant for spike initiation mechanisms in auditory afferents. Major assumptions are:
(a) a single trigger site and firing occurs when the transmembrane voltage reaches a fixed critical level; (b) postsynaptic voltage fluctuations are responsible for interspike-interval variability and are due to random times of occurrence of quantal synaptic inputs; (c) postspike recovery is due to a time-dependent decrease in the potassium conductance ($g_k$), i.e., an afterhyperpolarization; (d) cumulative after hyperpolarization is responsible for the lengthening of the mean interval following an interposed spike; (e) regular and irregular afferents differ only in the magnitudes of their afterhyperpolarization. The model predicts a stronger dependence of galvanic sensitivity on normalized-coefficient of variation of interspike intervals than is actually observed. The discrepancy can be explained by assuming a fourteen fold variation in the size of synaptic quanta characterizing different vestibular afferents.
IMPLEMENTATION OF THE CE-QUAL-R1 RESERVOIR MODEL AT THE
TRIANGLE UNIVERSITIES COMPUTATION CENTER

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The CE-QUAL-R1 reservoir model developed by the U. S. Army Corps of Engineers was adapted for use at the Triangle Universities Computation Center (TUCC).

This effort has now established two computer programs at TUCC which are available for simulation of reservoir ecosystems. CE-THERM-R1 simulates temperature, suspended solids, and total dissolved solids; CE-QUAL-R1 simulates these and other physical and chemical variables as well as biological components.

CE-THERM-R1 was run on a sample data set furnished by the Corps of Engineers. CE-THERM-R1 and CE-QUAL-R1 (in both the deterministic and Monte Carlo modes) were also run on sample data sets compiled from the literature for Falls Lake, North Carolina.

A list of reservoirs in North Carolina to which the model is most likely to be applicable was compiled.

Stochastic Differential Equations from a Modeling Point of View with Special Emphasis on Biological Applications

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Department of Mathematics*
1983 Ph.D. Dissertation, NCSU, Raleigh, N. C.

The stochastization of nonlinear models was studied. The models were assumed to be systems of n first order differential equations. The stochastic processes used as input to these equations were not restricted to white noise but were assumed to be generated by a system of d-n first order differential equations, nonlinear in their solutions but linear in their white noise input. The augmented system was studied as a necessarily degenerate d-dimensional Ito equation.

Some known theorems showing existence and uniqueness of solution processes to Ito systems of stochastic differential equations were extended to accommodate models not restricted by the traditional linear growth conditions yet allowing the above described degeneracy.

Boundary behavior of one-dimensional equations was studied and an easily applied sufficient condition for repelling boundaries was developed.

Numerical techniques were investigated for use with these augmented systems. These included a Monte Carlo simulation technique for use directly with the stochastic differential equations. The Kolmogorov-Smirnov statistic was used to obtain a confidence region for these Monte Carlo generated approximations.

Since the solution processes of Ito equations can also be described by means of partial differential equations (the forward and backward Kolmogorov equations), finite-difference techniques for use with these partial differential equations were investigated for comparison with the Monte Carlo routines.

All these developments were applied to various stochastizations of the logistic equation. The solution processes obtained from these new stochastizations of the logistic equation were shown to be more realistic than those satisfying earlier stochastizations of the equation.

*Co-major
LIFE TABLES FOR NONLINEAR DEATH PROCESSES

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Acta Biotheoretica 32:3-11 (1983)

The methodology concerning life tables has generally been based upon the assumption that the survival data from a natural cohort are binomially distributed around the values determined by the survivor function. The present investigation proved that such an assumption is valid only if the underlying death process is linear. Hence, if a contagious disease is the cause of a sufficiently large percentage of the deaths, the statistical analysis should not be based on the routine binomial model, but instead on the relevant model for the (nonlinear) death process.
MODELING OF EPIDEMIOLOGICAL DATA IN BANGLADESH

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In Teknaf, a remote area of Bangladesh, data have been collected on diarrheal diseases occurring in children below 6 years of age. The reporting forms also carry information about the history of past illnesses (including measles), nutritional status, age, etc.

On the basis of this type of data clinicians feel that attacks of shigellosis (a form of diarrheal disease) closely follow attacks of measles.

It has been suggested that these data could be analysed on the basis of a Cox regression model (proportional hazards model, or accelerated failure time model), which would allow us to take covariate levels into account. However, the data under consideration have several interesting events per lifetime, rather than one (in the simplest case one occurrence of measles and one occurrence of shigellosis, but often there are repetitions). Also, since the diseases under study are quite contagious, the usual assumptions underlying statistical inference are invalid (cf. preceding abstract).

The work is to concentrate on

1) extending failure time models to models allowing several signal events;
2) investigating epidemiological models as to the survivor distributions generated by them;
3) constructing a model relevant to the above-described situation.
ALTERNATIVE COMPUTATION OF CONDITIONAL EXPECTATIONS

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From some old statistical literature a little emphasized principle was distilled for the determination of a conditional expectation in a family of probability distributions: since the expected value of a conditional expectation is found by integrating the conditional expectation with respect to the parameter-indexed probability distribution of the conditioner, and the result is a function of the parameter, we can regard this parameter function as an integral transform of the conditional expectation. Thus we can find the conditional expectation by inverting the integral transform. Note that the kernel of this integral transform is provided by the probability density of the conditioner itself. The method works only if the conditioner is in a certain sense a sufficient statistic.

It is hoped that the derivation of classical tests, especially in exponential families, can be simplified by this method. There is also a basic problem as to which abstract conditions must be satisfied by the underlying $\sigma$-algebra on the one hand and the parameter space on the other hand in order that the structure of the parameter space be rich enough to yield the same result as the traditional application of the Radon-Nikodym theorem based on the $\sigma$-algebra.
A DYNAMIC MODEL FOR PLANT GROWTH: VALIDATION
STUDY UNDER CHANGING TEMPERATURES

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C. D. Raper, Jr.
Department of Soil Science
Annals of Botany (London) (to appear)

A dynamic simulation model to describe vegetative growth of plants, for which some functions and parameter values have been estimated previously by optimization search techniques and numerical experimentation based on data from constant temperature experiments, is validated under conditions of changing temperatures. To test the predictive capacity of the model, dry matter accumulation in the leaves, stems, and roots of tobacco plants (*Nicotiana tabacum* L.) was measured at 2- or 3-day intervals during a 5-week period when temperatures in controlled-environment rooms were programmed for changes at weekly and daily intervals and in ascending or descending sequences within a range of 14 to 34°C. Simulations of dry matter accumulation and distribution were carried out using the programmed changes for experimental temperatures and compared with the measured values. The agreement between measured and predicted values was close and indicates that the temperature-dependent functional forms derived from constant-temperature experiments are adequate for modeling plant growth to conditions of changing temperatures with switching intervals as short as one day.
Determination of DNA Fragment Size from Gel Electrophoresis Mobility.

Henry E. Schaffer

Computers and DNA Sequences: A Natural Combination.

Thomas R. Gingeras

The Role of Models in the Analysis of Molecular Genetic Data, with Particular Reference to Restriction Fragment Data.

W. J. Ewens

Statistical Analysis of Restriction Enzyme Map Data and Nucleotide Sequence Data.

Norman Kaplan

Analysis of Variation in Related DNA Sequences.

A. H. D. Brown and Michael T. Clegg

Inferring Evolutionary Trees from DNA Sequences.

Joseph Felsenstein

Convergent Evolution and Nonparametric Inferences from Restriction Data and DNA Sequences.

Alan R. Templeton

The Number of Polymorphic DNA Clones Required to Map the Human Genome.

D. Timothy Bishop, Christopher Cannings, Mark Skolnick and John A. Williamson.

Use of Restriction Fragment Polymorphisms as Genetic Markers.

Michael T. Clegg and Marjorie A. Asmussen
A statistical test for base composition

B. S. Weir
Department of Statistics

Nucleic Acids Research (in press)

A probability test for base composition in a small number of nucleotides is presented. Power calculations show that it is very difficult to distinguish between alternative base distributions unless a large number of nucleotides are observed. The likelihood ratio test does not appear to be appropriate for small sample sizes.
UNRAVELLING DNA INFORMATION

B. S. Weir
Department of Statistics

In The Fascination of Statistics,
Marcel Dekker, New York (in press)

Although recombinant DNA technology has allowed geneticists to look directly at the gene, instead of inferring its existence from morphological characters, the nature of DNA data requires the continued collaboration of statisticians. The complete unravelling of all the information in a DNA sequence is providing one of prime current examples of the fascination of statistics.
ESTIMATING F-STATISTICS FOR THE ANALYSIS OF POPULATION STRUCTURE

B. S. Weir and C. Clark Cockerham
Department of Statistics
Evolution (submitted)

Formulae are given for estimators for the parameters $F$, $\theta$, $f$ ($F_{IT}$, $F_{ST}$, $F_{IS}$) of population structure. As with all such estimators, ratios are used so that their properties are not known exactly, but they have been found to perform satisfactorily in simulations. Unlike the estimators in general use, the formulae do not make assumptions concerning numbers of populations, sample sizes or heterozygote frequencies. As such, they are suited to small data sets and will aid the comparisons of results of different investigators. A simple weighting procedure is suggested for combining information over alleles and loci, and sample variances may be estimated by a jackknife procedure.
A FORECASTING MODEL AIMED AT PREVENTING PINKEYE
THROUGH SHORT TERM BACTERIAL CONTROL

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Research attempts to determine the risk factors associated with outbreaks of Infectious Bovine Keratoconjunctivitis (Pinkeye) have consisted of statistical analysis of two sets of data. There is much disagreement in the literature about the etiological agent, incubation period, mode of transmission and other critical parameters involved in this eye disease of cattle. The modelling effort has been hampered by the fact that the literature contains virtually no parameter values or even raw data except for some qualitative remarks and some laboratory results which have not been reproduced and are disputed by other groups of researchers. Thus the modelling effort had to proceed from ground zero and is largely statistical rather than biomathematical in nature.

The two sets of data consist of:
1) survey forms distributed to farmers in the Fall for each of three years, 1979-81. The farmers report the level of disease and conditions on the farm, providing only one data point for each farm for each year. In addition many farmers do not keep records on the factors involved, so large variances in the quantitative data are inevitable. These surveys had not been intended to support a research effort, originally, but they constituted the only data available.
2) laboratory results of bacterial competition among the genera found in samples obtained by swabbing the eyes of the cattle.

In spite of the poor quality of the survey data a linear regression of pinkeye incidence against risk factors recorded in the survey was attempted. It seemed to indicate nine important variables, but resulted still in a rather high R-value. Only the data from those farmers who had participated for three years were used in the hope that their active interest was reflected in more reliable responses. The nine important variables were:
1) type of operation: winter stockers seemed to be most at risk.
2) interaction of age and breed: operations with a large percentage of calves and the Hereford breed group were most at risk.
3), 6), 7) type of forage: coastal bermuda and fescue significantly alter risk level.
4) region: South Piedmont most at risk.
5) level of fly population: the more flies, the higher the incidence of pinkeye.
8) year: this factor should be attributable to other factors, but not on the basis of these data.
9) treatment for IBR: increases risk level.
The results of Chi-square tests on the bacterial inhibition data were encouraging, in some cases significant at the 99.99% level. The presence of certain "inhibitor" bacteria, generally identified as Streptococcus, greatly reduces the severity of clinical signs of disease. Some cautious statements about the severity of disease associated with M. Bovis versus Neisseria and their hemolytic versus nonhemolytic forms as well as threshold levels required to produce disease do seem possible, although the data points are relatively few.
Data were obtained in 1979 and 1980 on various populations, principally Spot and Croaker, in Rose Bay, an arm of the Pamlico Sound bordering on the North Carolina coast. Periodic trawl samples were studied as to numbers, lengths and locations of fish obtained. Our work has been concerned with developing a model which can be used to estimate certain rates - growth, survival, movement between locations, immigration and emigration, and chance of catching - for the individual fish, working from the existing data. A Leslie-type model has been developed which predicts numbers of fish in the successive length categories, relative to parameters reflecting the above-mentioned rates. Numerical procedures are used to obtain least-squares estimates of the model parameters. The statistical "bootstrapping" technique will be used to assess variability in the estimates.
Black-footed ferrets (Mustela nigripes) are exceedingly rare and only a single extant population in Wyoming is known. Tracks in the snow and direct observations have provided data on activity and show that a ferret can travel from 0 to almost 7 km and can move almost 50 l of soil from prairie dog (Cynomys spp.) burrows in a night. We constructed an additive model to estimate ferret energy expenditure, including energies for running, digging, investigating burrows, and thermoregulation. From our field data, we estimate that ferrets expended an average of 130 kcal/d during winter, 1982. We used the Siberian polecat (M. eversmanni) as a biological model for the endangered ferret to estimate energy and nutrient acquisition from 2 ferret prey species. Gross energy content, proximate analyses and utilization by the polecats of the 2 prey did not differ and were comparable to results for other carnivores. The polecats consumed an average of 125 kcal/d during feeding trials, which is equivalent to 104 metabolizable kcal/d. Therefore ferrets must eat at least 20 prairie dogs during the 4 winter months (December-March). During summer months ferrets might need to eat prairie dogs at up to 6 times this rate. Our results have conservation implications, including the possibility of very low natural ferret densities in prairie dog towns. We urge caution in prematurely concluding that a prairie dog town does not support ferrets.
COMPETITION AND COEXISTENCE IN MUSTELID COMMUNITIES

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Mustelid species guilds are large but competition between mustelid species appears limited except in the genera Martes and Mustela. Several different nonequilibrium community models indicate that 2 or more Mustela may coexist temporarily due to different reproductive adaptations, differential predation on different prey, prey population fluctuations, and predation on Mustela by other predators. Long-term coexistence only occurs through local extinction and recolonization.
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