ABSTRACTS OF COMMUNICATIONS

Proceedings of the Twenty-Second Meeting of the AFRC Modellers' Group

EDITED BY

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This group, which is concerned with the applications of mathematics to agricultural science, is sponsored by the Agricultural and Food Research Council. It was formed in 1970, and has since met at approximately yearly intervals in London for one-day meetings. The twenty-second meeting of the group, chaired by Professor J. M. Forbes of the Department of Animal Physiology and Nutrition at the University of Leeds, was held in the Wellcome Meeting Room at the Royal Society, 6 Carlton House Terrace, London on Friday, 10 April 1992, when the following papers were read.

A mathematical model for the neural control of luteinizing hormone secretion. D. BROWN, A. E. HERBISON, G. LENG AND R. W. MARRS. *Statistics Group and Neuroendocrinology Department, AFRC Institute of Animal Physiology & Genetics Research, Babraham Hall, Cambridge CB2 4AT, UK*

A substantial release of luteinizing hormone (LH) into the bloodstream is the precursor of ovulation in most mammals. Also when separated from the influence of ovarian steroids in the ovariectomized animal, LH is typically released in regular brief pulses. In our current study, a mathematical model has been constructed of the means by which luteinizing hormone releasing hormone (LHRH) neurones achieve such a pulsatile pattern of LH release in ovariectomized animals, and a preovulatory surge of LH in normal animals. Utilizing an analogy with the Fitzhugh–Nagumo model of the firing of a single neurone (Fitzhugh 1961; Nagumo *et al.* 1962), this model is centred on a feedback loop between $v =$ the average electrical activity of the LHRH neurones and $w =$ the local concentration of gamma-aminobutyric acid (GABA). The excitability of the system necessary for the pulsatile behaviour in the ovariectomized animals is achieved by (i) the LHRH neuronal activity – when separated from the controlling influence of GABA – following a bistable model: if stimulated below the threshold, v_1, v returns to zero, whereas stimulation above this threshold causes a movement to the level $v = v_2$; (ii) as LHRH rises, GABA release is stimulated, which in its turn abolishes LHRH activity. Just prior to the LH surge in normal animals, GABA levels fall, reflected in the model by a reduction in the basal level of GABA. Like the Fitzhugh–Nagumo model, when the neurone is subject to a continuous positive current this results in continuous pulsing, in this case of LHRH followed by a surge of LH. Some possible alternative models are also reviewed.

FITZHUGH, R. (1961). Impulses and physiological states in models of nerve membrane. *Biophysical Journal* **1**, 445–466.

NAGUMO, J. S., ARIMOTO, S. & YOSHIZAWA, S. (1962). An active pulse transmission line simulating a nerve axon. *Proceedings of the Institute of Radio Engineers* **50**, 2061–2070.

Animal disease regulation as a trade barrier: Argentinean beef and foot-and-mouth disease. L. BARROS[1] AND S. MCCORRISTON[2]. [1]*Institute of Mathematics & Statistics, University of Kent, Canterbury, Kent, CT2 7NF, UK,* [2]*Agricultural Economics Unit, University of Exeter, Exeter, Devon EX4 6TL, UK*

This paper focuses on the role and economic impact of animal health restrictions in the international beef market. Mathematical conditions are derived for the general case when increased exports from a country which has eradicated an endemic animal disease such as foot-and-mouth disease (FMD) affect world beef prices. These conditions evaluate the impact on total revenue levels in the situation before and after disease eradication, depending on the direction of price changes in the countries imposing an importing ban and the rest of the world (ROW) market. The model shows that the critical issue is the supply–price elasticity in the ROW market. A case study is used to evaluate the economic impact of importing bans imposed by major importers on fresh beef products from FMD endemic areas, the USA and Argentina being used as importing and exporting countries respectively. In this paper, we will assume that the effect on export earnings represents the most important economic loss due to the disease. McCauley (1983) reports relatively small production losses for Brazil, a country with a long history of endemic FMD in a low-productivity beef sector. These losses also reflect the negative impact of other health problems and low management skills in traditional production methods. In addition, a FAO study estimates that direct production losses in Argentina due to FMD represent only 5% of total losses, the remaining 95% being associated with the loss of potential export earnings (FAO 1984). This paper shows that, under certain assumptions, simple redirection of exports to high-price markets will not justify the cost of an FMD-eradication programme in economic terms. A major effort must be made towards increasing beef exports at the expense of the domestic consumer, at least in the short term. The analysis also suggests that a global approach must be used to evaluate the economic impact of animal health regulations on the international beef market. In particular, removing animal health regulations is likely to affect relative market shares as well as world beef prices.

Food and Agriculture Organisation (1984). *Informe del seminario regional de la FAO sobre epizootiologia y economia de la sanidad animal*, Proceedings of FAO Meeting, Lima, Peru, 1984.

McCauley, E. H. (1983). *Animal diseases in developing countries: technical and economic aspects of impact and control*, Agricultural Policy Unit Technical Notes No. 7, World Bank, Washington DC.

Modelling the performance of a non-steady state continuous aeration plant for the treatment of pig slurry. C. H. BURTON. *Silsoe Research Institute, Wrest Park, Silsoe, Bedford MK45 4HS, UK*

Prediction of the performance of a continuous aeration process, where steady state is not assumed, was attempted using a combination of engineering and microbiological concepts. Performance was defined in terms of the reduction of the COD (chemical oxygen demand) value of the slurry, from which estimates of other factors, such as the post-treatment storage time free from offensive odours, can be made. It was also necessary to predict the temperature of the aerated slurry, both as an intermediate step in estimating the COD level, and also in identifying occasions when it could disrupt microbial activity, i.e. when it fell outside the range for mesophilic bacteria (10–47 °C).

The two models developed were based on the principles of running means and hourly increments respectively. The former represented a simpler idea which applied steady-state correlations for heat balances and COD predictions, using values averaged over the preceding days. The second model was based on a Monod-type function with an exponential temperature dependence (Arrhenius), which was then combined with incremental heat balances to predict temperature changes. The various constants for both models were set up using temperature and COD data from farm-scale aeration trials. The predictive accuracy of the models was then evaluated on data from a separate 2000 h trial in which the operating conditions had been varied throughout.

Both models predicted temperatures and COD reductions well, generally to within 20% of the actual value. The relative sophistication of the incremental model provided no improvement in predictions. This may be the consequence of imprecise and incomplete data, and highlights the problems of a more rigorous approach to a complex microbial system.

Environmental instability in heterogeneous domains. P. K. MAINI, D. L. BENSON AND J. A. SHERRATT. *Centre for Mathematical Biology, Mathematical Institute, 24–29 St Giles', Oxford OX1 3LB, UK*

Species interaction models have been widely studied to investigate the phenomena of population fluctuations and extinction. To a great degree, these models have assumed that the environment is spatially homogeneous, although discrete 'patch models' suggest that movement between patches has important global implications. However, in continuous models the effect of inhomogeneities in the habitat has received relatively little attention, although the threat posed to nature reserves by partly disrupting the habitats of competing species has been studied.

A general deterministic predator–prey dispersal model is studied (Benson *et al.* 1992). The effect of spatially non-uniform dispersal rates, due to environmental variability, is investigated by taking the diffusion coefficient of one of the species to vary across the domain. The results show that such inhomogeneous dispersal rates can give rise to a range of different spatial patterns in population density, including pattern localized in one part of the domain. The parameter space wherein different types of behaviour occur can be mapped out.

The model is used specifically to investigate 'environmental instability'. It is shown that, in the appropriate parameter regime, the solutions of a predator–prey model can be unstable to changes in the dispersal rates. That is, a model which exhibits stable uniform densities can be driven unstable by changing the dispersal rate of one species in only a small portion of the domain. This results in the population densities assuming a stable spatially non-uniform pattern throughout the domain. The conclusion is made that the effect of localized environmental changes can propagate into the domain, creating a global change.

D. L. B. acknowledges the Wellcome Trust for a Prize Studentship in Mathematical Biology.

BENSON D. L., SHERRATT, J. A. & MAINI, P. K. (1992). Diffusion driven instability in an inhomogeneous domain. *Bulletin of Mathematical Biology* (in press).

Modelling cold hardening and dehardening in *Lolium*. A. P. GAY AND C. F. EAGLES. *AFRC Institute of Grassland and Environmental Research, Plas Gogerddan, Aberystwyth, Dyfed SY23 3EB, UK*

The ability of plants to survive at low temperatures is dependent upon the acquisition of cold hardiness. The level of hardiness generally increases as temperatures fall in the autumn and rises in the warmer temperatures of spring, and changes in the winter in response to the actual temperature. This presents a problem when comparing cold hardiness of field-grown material, since temperature fluctuations change hardiness. Thus experiments in controlled environments have been used to characterize thermal responses for hardening and dehardening using a freezing test to assess cold tolerance as the temperature that kills half a population of plants (LT_{50}). These experiments are difficult to analyse, since both time and temperature of acclimation influence LT_{50}. We have developed models which relate changes of cold-hardiness to time and temperature in varieties of *Lolium perenne* and *L. multiflorum*. Parameters describing features of biological interest that simplify comparisons between varieties and species are obtained from the model.

Initially two models relating hardening and dehardening to temperature were considered (Gay & Eagles 1991). Both models showed an exponential decline in the rate of change of LT_{50} from an initial to its final value. The first model related this decline in LT_{50} to thermal time accumulated below a fitted threshold temperature and, although a good fit to the hardening data, it did not fit the dehardening data. The second model used an exponential time course of change in LT_{50}, but the final LT_{50} was defined as being logistically related to temperature. This model fitted the dehardening and hardening data well, and was used to estimate values for the initial rates of hardening and dehardening at a specified temperature, the maximum potential for hardening and dehardening and the extent to which this was achieved in a given time.

GAY, A. P. & EAGLES, C. F. (1991). Quantitative analysis of cold hardening in *Lolium*. *Annals of Botany* **67**, 339–345.

A temperature-based simulation method for forecasting the times of peak periods of attack by insect pests of horticultural crops. K. PHELPS AND R. H. COLLIER. *Horticulture Research International, Wellesbourne, Warwick CV35 9EF, UK*

The rates at which insects complete their life-cycles are mainly dependent on temperature, and a range of models has been developed for using field temperatures to forecast peak periods of insect activity. Many of these models predict development times from relationships between the mean rate of development and constant temperature, derived in controlled experiments. However, few of the models take account of intra-population variability in development time, although this is a major concern, particularly where several generations of the pest occur in a season.

Frequency distributions of insect development time within a population are usually skewed towards the slower-developing insects, whereas distributions of development rate are often symmetrical about the mean. Furthermore, coefficients of variation of times or rates are relatively independent of temperature, and thus a single temperature-independent distribution can be used to describe the distributions at all temperatures. This is known as the same-shape property (Curry *et al.* 1978).

A flexible system has been developed using Monte-Carlo simulation to include intra-population variability, which can also accommodate other aspects of the developmental biology of insects, for example different thresholds for the induction of diapause or aestivation. It is being used to provide a practical pest forecasting system (Collier *et al.* 1991, 1992) in the UK for cabbage root fly (*Delia radicum*) and carrot fly (*Psila rosae*), whilst those for the bronzed-blossom beetle (*Meligethes aeneus*) and the large narcissus fly (*Merodon equestris*) are still in the development stage.

COLLIER, R. H., FINCH, S. & PHELPS, K. (1991). A simulation model for forecasting the timing of attacks of *Delia radicum* on cruciferous crops. *European and Mediterranean Plant Protection Bulletin* **21**, 419–424.

COLLIER, R. H., FINCH, S. & PHELPS, K. (1992). The feasibility of using models to forecast carrot fly attacks in commercial crops. *Bulletin of the International Organisation for Biological and Integrated Control of Noxious Animals and Plants, West Palaearctic Regional Section* (in press).

CURRY, G. L., FELDMAN, R. M. & SHARPE, P. J. H. (1978). Foundations of stochastic development. *Journal of Theoretical Biology* **74**, 397–410.

Aggregation and incidence of plant disease. G. HUGHES. *Institute of Ecology and Resource Management, University of Edinburgh, West Mains Road, Edinburgh EH9 3JG, UK*

Many ecological data exemplify the empirical law of Taylor (1961) describing a linear relationship between the logarithms of the variance and mean of population density of a species, estimated from groups of replicate samples. This 'power law' has been used as a statistical description of aggregation, for the formulation of variance-stabilizing transformations in the analysis of count data, and as the basis of a behavioural model of species' spatial dispositions. Sample population data collected in binary form, such as the incidence of plant disease (proportion of individuals infected), have a different type of variance–mean relationship: as the mean proportion of individuals diseased approaches its maximum value, the variance decreases (Madden 1989).

Taylor's law is usually written $\log(v) = \log(a) + b\log(m)$ [eqn (1 *a*)], in which v and m are, respectively, the observed variance and mean of population density of a species and a and b are parameters to be estimated. However, we can think of the power law as describing a relationship between two variances: the observed variance (v) and the variance that the population would have if it were randomly (Poisson) distributed (v_r). Thus we can write: $\log(v) = \log(a) + b\log(v_r)$ [eqn (1 *b*)] without sacrificing any of the utility of eqn (1 *a*), since $v_r = m$ for population count data. For binary data characterized by the binomial distribution, $v_r = p(1-p)/n$, where n is the (constant) sample size and p is mean incidence ($0 \leqslant p \leqslant 1$).

Equation (1 *b*) provides a basis for an analysis which can be thought of as a binary data analogue of Taylor's power law. Disease incidence data from virus-infected crops of tobacco are used to illustrate this analysis, which has some interesting properties. It provides a statistical description of aggregation and allows the formulation of appropriate variance-stabilizing transformations. In addition, the problem of finding a probability distribution with an exact power law variance–mean relationship at all values of mean incidence is easily resolved.

MADDEN, L. V. (1989). Dynamic nature of within-field disease and pathogen distributions. In *Spatial Components of Plant Disease Epidemics* (Ed. M. J. Jeger), pp. 96–126. Englewood Cliffs, New Jersey: Prentice-Hall.

TAYLOR, L. R. (1961). Aggregation, variance and the mean. *Nature* **189**, 732–735.

An architectural model of bracken growth.
T. R. BUTLER-STONEY, R. J. HAGGAR, N. R. SACKVILLE-HAMILTON AND A. P. GAY. *AFRC Institute of Grassland and Environmental Research, Plas Gogerddan, Aberystwyth, Dyfed SY23 3EB, UK*

In western Europe, bracken (*Pteridium aquilinum*) is an aggressive, vigorous plant capable of spreading into improved grassland and heather moorland. De-intensification of agriculture coupled with predicted climate change could increase bracken colonization through rhizomatous spread. Non-chemical control measures require improved understanding of rhizome dynamics and carbohydrate fluxes as influenced by grazing and climate perturbants.

Using existing data, supplemented with that emerging from eco-physiological studies, a model has been constructed to interpret the complex rhizome system (consisting of a continuous range of types from shallow and thin with short internodes to deep and thick with long internodes) in terms of the physiology of individual nodes. In this model each node is connected to one parent node and two daughter nodes (apical and lateral growth). Levels of mobile and stored carbohydrate are maintained for each node, and the connections between nodes allow translocation through branching rhizomes. Competition is modelled by making photosynthesis a function of the number of leaves in each half-metre square of soil surface. As the simulation proceeds, nodes are added to and removed from the model and the connections between rhizome fragments change as the model brings about death of the ancestral nodes. Thus the development of the interconnected mass is modelled from the behaviour of individual nodes.

This model was produced using object-oriented programming in Turbo C^{++}. Object-oriented programming allows separate definitions of individual components such as position and carbohydrate storage to be combined into the definitions of the model node. Additional features of the real plant can be added to the model, with minimal disruption to the rest of the program. The model can readily incorporate other appropriate factors of interest. As such, it will be helpful for predicting the plant community and landscape consequences of bracken invasion.

Analysis of bracken spread using geographic information systems coupled with an expert system.
D. MILLER. *Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB9 2QJ, UK*

The encroachment of bracken on to areas of rough grazing and improved pasture with a resultant decrease in agricultural return from such land is widespread in upland Scotland, Wales and areas of England (Taylor 1986), and its areal extent is increasing by up to 3% per annum (Birnie & Miller 1987). The targeting of resources for the control of bracken is difficult because of the uncertainty about the extent of current bracken presence and where it is spreading most rapidly.

Geographic information systems may be employed in the mapping of vegetation for using both spatial data and aspatially represented knowledge (Lowell 1991). Satellite imagery, digital terrain data and small-scale soil and landform data provide spatially expressed inputs, whereas measured vegetation relationships with ecological variables, vegetation dynamics and vegetation succession are reported aspatially. Changes in vegetation cover may be predicted from vegetation mapping and knowledge of environmental factors influencing vegetation.

An expert system shell – SBS (Baldock *et al.* 1988), written in POP–11 – is presented, which is used as a framework within which to develop an approach to predicting where bracken is likely to be present, and the likelihood of bracken encroaching on neighbouring vegetation. Selections of analysis techniques to be used are based upon opinions expressed in relevant literature indexed against appropriateness, efficiency and robustness. Information specific to individual experts (e.g. soil type details) is held in a frame structure which manipulates the object-referenced data, and access is made to the 'raster'-format spatial datasets by Fortran routines initiated by the expert system.

Development of the system is in an area of central Scotland where bracken has been identified as being a problem. Predictions of where land is most susceptible to bracken encroachment are made which provide a basis for assessing what resources are required for eradicating or controlling bracken in upland Scotland.

BALDOCK, R. A., IRELAND, J. & TOWERS, S. J. (1988). *SBS Users Guide*. MRC Clinical and Population Cytogenetics Unit, West General Hospital, Edinburgh, internal report.

BIRNIE, R. V. & MILLER, D. R. (1987). Lessons from the bracken survey of Scotland: the development of an objective methodology for applying remote sensing techniques to countryside mapping. In *Proceedings of Monitoring Countryside Change* (Eds W. Adams & J. Budd), Silsoe College. Chichester: Packard Publishing Ltd.

LOWELL, K. E. (1991). Utilizing discriminant function analysis within a geographical system to model ecological succession spatially. *International Journal of Geographical Information Systems*, **5**, 175–192.

TAYLOR, J. A. (1986). The bracken problem: a local hazard and global issue. In *Proceedings of Bracken '85, Bracken Ecology, Land Use and Control Technology* (Eds R. T. Smith & J. A. Taylor), pp. 57–64. University of Leeds: Parthenon Publishing.

Kriging temperatures in Scotland using elevation as external drift. G. HUDSON. *Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB9 2QJ, UK*

Land-use research involves the formulation and testing of models for land evaluation, land suitability and crop yield at the regional or district scale. Such models provide the physical inputs necessary to make economic forecasts about the returns from alternative land uses. This research needs information about the space and time variability of soil and climatic properties to be effective. Land evaluation systems are multivariate classifications that use information about the soil, topography and climate to make predictions about the potential of different areas of land for specified uses. Crop yield models use the same data to estimate crop performance. Modelling the seasonal and spatial variation of climatic variables is therefore important for land evaluation and yield prediction.

Temperature data are sparse in Scotland, with *c.* 150 climate stations covering a domain extending 600 km from north to south and 300 km from west to east. Because temperature is universally correlated with elevation, it is possible to make use of this relationship by using elevation as external drift to krige temperatures. The underlying hypothesis is that the regression of temperature on elevation is linear.

The study was carried out in three stages: (i) structural analysis and kriging of climate station elevations, (ii) structural analysis and kriging of temperatures and (iii) kriging of temperatures using elevation as external drift.

In summary, the temperatures are non-stationary in different directions in winter and summer, but there appear to be stationary periods in spring and autumn. The parameters of the linear regression with elevation may not be constant over the whole domain when using a moving neighbourhood. Kriging temperatures with elevation as external drift gives estimates of temperature which are closer to reality than those obtained by kriging temperatures using only standard drift functions. The implications for land evaluation or crop suitability models are that more accurate estimates can be used where the sensitivity to temperature is high.