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USE OF MODELS IN THE STUDY OF INSECT POPULATION DYNAMICS

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Population ecology and, more specifically, population dynamics deal with problems that are characterized by high degrees of complexity and uncertainty. The complexity results from the fact that population behavior is the outcome of processes occurring at two different levels of organization: individual organisms and communities. Uncertainty stems from two sources: (1) a wide knowledge gap concerning the exact nature of many of the key processes involved in population regulation; and (2) the overwhelming number of factors that can have direct or indirect influences on population processes, which confer to populations an often erratic ("noisy") pattern of change. This stochasticity is believed to result from the combined influence of a large number of extrinsic factors that are either too poorly understood or too complex to take into specific account and are lumped together into the category of so-called "random perturbations" acting on the population system.

Complexity and uncertainty have made the use of models a very important tool in the conduct of population studies. The objective of population ecology is to discern and understand the causes of patterns of population change (Royama 1996). Such understanding can then be applied to predict future changes or modify them by management.

In selecting the topics for this workshop, we wanted to contrast two different types of models used in the study of population ecology: deductive and descriptive models. Deductive models are developed as a formal series of mathematical arguments derived from a few, clearly stated, premises and assumptions. Such models are true mathematical models in the sense that the procedure used to derive them (and often to study them) is essentially mathematical. They are often extremely powerful at clearly defining basic concepts such as persistence, stability, regulation, or density dependence itself (see Royama 1992). Two presentations in this workshop focused on the application of such models (time-lagged, autoregressive

stochastic processes) in the analysis and interpretation of observed population patterns (population time series).

Descriptive models are built from more or less detailed knowledge of selected ("key") processes in the ecology of a particular species. Here, mathematics are used more for their descriptive convenience than as a tool for logical deduction or induction. In fact, most such descriptive models use mathematics as an intermediate step towards computer programming. The primary use of descriptive models is as a communication tool to summarize the modeller's understanding of a population system and to generate or test hypotheses about emerging model behavior. Two presentations were devoted to this type of model: mountain pine beetle and spruce budworm population dynamics.

The first point of discussion, which became rather heated at some point, was the relative usefulness of the two types of modeling approaches. The main issue was the lack of a simple line of mathematical logic in the structure of descriptive models. The relative complexity of such models makes it difficult to quickly grasp the implications of model premises, assumptions, and equations. By contrast, deductive models are developed along a single, formal sequence of mathematical logic, so that the implications of all steps in their development are more immediately obvious to the mathematically inclined (which is not the norm among ecologists). In the case of a complex descriptive model, the audience has to trust the modeller's ability and art, and his/her ability to discover the main implications of the formulation used. However, judging from the amount of discussion that took place around each individual presentation, descriptive models (particularly the mountain pine beetle model) stimulated by far the most interest. This may have been partly due to the fact that their formulations and implications had to be explained in more detail after the presentation. However, it also may have been the result of the greater amount of biological detail involved in their description which ecologists could discuss.

A second point of discussion focused on the use of the term “noise” when referring to the influence of external factors lumped into the “random variable” category. It was suggested that “noise” should be restricted to the idea of “error” around population estimates (a strictly additive term), and that “perturbations” should be used when referring to factors that have an impact on the TRAJECTORIES adopted by the population processes rather than just adding fuzziness to that trajectory. In most population processes where density dependence must exist, the influence of external factors is filtered through the population system and becomes an intrinsic part of the population trajectory.

In summary, this was a very interesting workshop, at the end of which peace was made between proponents of diverging modelling approaches to population studies. Luckily, nobody suggested that models were not useful. Also, the issue of “simple” vs “big ugly” models (Logan 1994) was avoided altogether.

ROLE OF MODELS IN POPULATION STUDIES

T. Royama^a

Population studies depend heavily on the use of models. There are different types of models: descriptive, explanatory, deterministic, stochastic, linear, nonlinear, etc. These serve different purposes at different levels or stages of progress in research. A model is, by definition, not a real thing; it is a paradigm or idealization of essential features that we wish to abstract from observations. It is important to use a model within the scope it is designed for. An uncritical application and over-interpretation of a model results in distorted perceptions of population processes. [This presentation discussed the bases and caveats of time series analysis applied to population census data, by describing and applying increasingly “complex” linear stochastic processes to mimic observed time series with a view of inferring the underlying regulation structure.]
[]Added by J. Régnière.

DETECTION OF DELAYED DENSITY DEPENDENCE IN ECOLOGICAL TIME SERIES: EFFECTS OF AUTOCORRELATION IN EXOGENOUS FACTORS

A. M. Liebhold^b and D. W. Williams^c

Delayed density-dependence is important in regulating animal populations, and recent work has suggested analytical methods for its detection in population censuses. However, theory suggests that autocorrelation in an exogenous factor, such as weather, which acts in density-independent fashion, may give the appearance of delayed density dependence. We examined this question through stochastic simulations of a linear difference equation model and a discrete version of the logistic model, neither of which contained lags. The random term for the simulations was modeled as a first order autoregressive process. We varied the parameters that determine direct density dependence in the population models and autocorrelation and random variation in the exogenous factor, and subjected the resulting series to time series analysis and regression analysis. Using these methods, many simulated series were diagnosed with significant delayed density dependence, and the frequencies of significant cases also increased as the parameter for direct density dependence increased in the linear model, and decreased as r increased in the logistic model. We concluded by discussing generalist predators and weather as possible autocorrelated exogenous factors and urged caution in the use of single-species models and analyses in predicting populations and diagnosing their regulation.

TEMPORAL EVOLUTION OF SPATIAL PATTERNS IN MOUNTAIN PINE BEETLE OUTBREAKS

James Powell^d

We discussed how aggregative population movement can generate spatial heterogeneity, using a model for the chemotactic movement of the mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) and its ‘predator-prey’ interaction with host species, in particular lodgepole pine (*Pinus contorta* Douglas). Since the prey species is immobile, the predator disperses only once a year, and the details of the