Gambling for existence

Reddingius, Joannes

Part 1

Chapter 1. The science of population ecology is briefly described as the author understands it. The concepts "population", "population density", and "environment" as they will be used in this paper are defined. The aim and scope of the paper are described: it will be mainly concerned with the controversy about the "regulation" of population density by "density governing factors". It will be attempted to formulate opposing theories as alternative hypotheses that can be tested by observation. In Part 2, some statistical problems with respect to this testing of hypotheses will be discussed.

Chapter 2. The controversy concerning the regulation of population densities is briefly described and commented on. A deterministic mathematical theory is given on the basis of a few simplifying assumptions which in the author's opinion do not invalidate the argument. The mathematical theory, despite its restriction to these assumptions, is more general, though less detailed, than earlier mathematical models. The influence of all environmental and populational factors on density is measured by the net reproduction coefficient. Necessary and sufficient conditions for population density to remain between positive limits are stated in terms of relationships between net reproduction and density. It is shown that if population density approaches a limit when time goes to infinity, this limit is an equilibrium density. The arithmetic and geometric time averages of density then will tend to the same limit.

Chapter 3. Population density as a function of time is best regarded as a realization of a stochastic process. For simplicity of the argument the discussion is restricted to the case where this stochastic process is a Markov chain with stationary transition probabilities. The state "density = 0" presumably can be reached from all other states and is absorbing. It follows that population density tends to zero with probability 1 even if there are "density governing factors" operating on it. This diminishes the validity of the argument that populations must be governed because otherwise they would become extinct in the long run.

Chapter 4. The concept of "density dependence" as it is used in the ecological literature must be distinguished from stochastic dependence. Definitions of ecological density dependence are given in terms of stochastic dependence. If net reproduction is density-independent in the ecological sense, it will nevertheless be stochastically dependent on density, although for large populations this may be negligible.

For first-order Markov chain populations, a necessary condition for population density to remain between positive limits for a long time is stated in terms of transition probabilities; a similar condition in terms of conditional expectations is proved to apply when the first condition holds. A sufficient condition cannot be found as extinction is inevitable according to Chapter 3. If time to extinction is given to be long, the probability distribution of density in a certain conditional sense and under plausible assumptions tends to a limit distribution as time goes on. This implies that the arithmetic time average of density will in a certain conditional sense tend to a limit in mean square, hence also in probability. This might be called a "tending to equilibrium", but such an equilibrium is a concept quite different from "equilibrium densities" as occur in certain deterministic models.

Chapter 5. A scheme of admissible hypotheses (i.e. hypotheses that can be tested by observation) is discussed. Extinction of populations is a subject needing further investigation. A hypothesis stating that population densities fluctuate between "reasonable" limits for a long time without density governing factors playing an important role appears to be not so illogical as was thought by certain theorists. Our information concerning the behaviour of net reproduction at very high or very low densities for most field populations is insufficient. Heterogeneities within the population (age and genetic differences for example) as well as in the environment may have a stabilizing influence on density fluctuations. A correlation between environmental conditions and density can be expected to exist even when density is not regulated towards a definite equilibrium value corresponding to those conditions. Metaphorically, species might be said to gamble for existence.

Chapter 6. It is argued that scientific experiments aim at either rejecting a null hypothesis or accepting it, and not merely at rejecting null hypotheses. Accepting a null hypothesis implies accepting a number of other hypotheses that do not differ much from the null hypothesis.

Part 2

Chapter 7. Statistical methods for testing hypotheses are indispensable in ecological work. The ecologist should not only have a working knowledge of such methods, but also a good insight into the mathematical models presupposed by these methods.

Uncritical application of textbook recipes can lead to erroneous conclusions.

Chapter 8. Some examples of statistical misconceptions and controversies are discussed. Correlation and regression analysis have been applied to field data in order to investigate whether net reproduction is negatively density-dependent. Although the results in some instances do suggest interesting correlations, the available data are not appropriate for this kind of analysis, and in some cases tests have been based on erroneous assumptions.

Chapter 9. A discrete-time mathematical model is discussed where the regression of the logarithm of net reproduction on the logarithm of density is linear. Whether or not net reproduction is negatively density dependent can be stated in terms of the parameters of the model which therefore is appropriate to base statistical significance tests on. The model is, however, not quite satisfactory from a biological point of view. It is hoped that in some cases it will provide a useful approximation.

Chapter 10. Some statistical tests concerning parameters of the model of Chapter 9 are discussed. The following possibilities are considered:

1. A test based on the likelihood ratio. Significance points for this test are unknown and were estimated by Monte Carlo simulations.
2. A test based on the serial correlation of the densities. Significance points are unknown, and Pearson curve approximations to the distribution of the test statistic seemed inappropriate.
3. A test based on the serial correlation coefficient of the logarithms of the net reproduction coefficients.
4. A test based on the sample regression coefficient of the logarithms of densities at odd times (t=1,3,5,...) on the logarithms of densities at even times (t=0,2,4,...) when the latter are treated as being given.

The first two tests seem to have greater power than the last two, but the latter have the advantage that exact significance points are available.

Although the model used in these tests in some respects lacks biological realism, the tests might be sufficiently robust against moderate and uninteresting departures from the model to be useful in practice. The test based on the serial correlation coefficient of log(net reproduction) is not wholly unambiguous as regards the interpretation of its result: a significantly negative correlation can arise in other ways than the one envisaged here.

Chapter 11. Some suggestions for distributionfree tests are given. A test defined on the set of all permutations of the net reproductions found in a particular instance seems to be feasible, the null hypothesis supposing that all permutations are equally probable, and the critical region of the test consisting of those permutations for which the range of the resulting densities is smallest; but this test at the moment will be difficult to apply in practice for computational reasons. Tests based on the number of runs can be applied but they will not be very powerful. A distributionfree analogue of the test based on the circular serial correlation coefficient of log(net reproduction) can be applied and may be useful in some instances.

Chapter 12. In practice it is often impossible to obtain exact measurements of population densities over a series of years. For populations for which the first-order Markov model might be appropriate, densities usually have to be estimated from samples. This introduces a source of error which may invalidate the significance levels of the tests discussed in the preceding chapters. Unfortunately, this works the wrong direction: the significance level is underestimated, and the null hypothesis is too often rejected. Under certain conditions and for long series, a correction factor may be applied in the computation of the test statistics when estimates of the sampling error are available.

In addition to this, it should be realized that the model may be wholly inappropriate. The densities of even uninvoltine insects need not be realizations of first-order Markov chains, as they sometimes show cycles over several years more regular than could be expected to occur in a first-order Markov series.

Some examples are discussed on the basis of published population data. Evidence in favour of the "governed density" hypothesis is not very convincing as yet, but some results do indicate that collection of more data could lead to acceptance of this hypothesis.