Introduction

The thesis put forward in this issue of *Philosophical Transactions* is that population growth rate is the key unifying variable linking the various facets of population ecology. It is argued that analyses of population regulation, density dependence and the effects of environmental stress, are all best undertaken with population growth rate as the response variable. The argument is essentially a reductionist one. External factors such as limitations of food availability or other resources impact individuals, determining individual birth and death rates. And population growth rate is the integral of individual birth and death rates. So if we want an understanding of the mechanisms determining population growth or decline, this can be summarized by identifying the determinants of population growth rate and characterizing their effects on population growth rate. By using such models with strong *a priori* justification as the basis for analysis, more insight is gained into the fundamental processes of population ecology. These should not only improve the quality of the underlying science, but also increase the realism and accuracy of prediction in key applied areas. For conservation biologists, human demographers, wildlife managers and ecotoxicologists, it is of practical importance to know whether populations are increasing or declining, and to identify the factors that determine growth rates.

The research programme outlined above has generally been approached in three main ways, each incorporating observations, experiments and theoretical analyses. These are contrasted as alternative paradigms, with case studies, in the papers by Sibly & Hone (2002) and Hone & Sibly (2002). Those seeking a reductionist understanding of the effects of external factors on population growth rate are working within a *mechanistic paradigm*. The net effect of the external factors acting on individuals may, however, be a simple relationship between population density and population growth rate, and the study of such relationships constitutes a *density paradigm*. Others have concentrated on elucidation of the link between population growth rate and individual life histories, and this can be seen as a *demographic paradigm*. Note, however, that there are also studies that are very successful in quantitative prediction of population growth and decline, without requiring the explicit calculation of population growth rate as an intervening variable (see Clutton-Brock & Coulson 2002; Sutherland & Norris 2002).

Before describing the structure and contents of this issue of *Philosophical Transactions*, it is important to note that measured values of population growth rate are specific to the environment in which they are measured. This may seem obvious but it is of great importance and constitutes one of the major themes running through the papers presented here. Change the environment and the value of population growth rate will change, and there may also be changes in the relationship between population growth rate and the factors that determine it. We shall return to this point.

The simplest line of attack on the determination of population growth rate is to look for and characterize the effects of population density (the 'density paradigm') in a constant environment, and we begin with analyses of this type. Populations for which there is a negative relationship between density and population growth rate are regulated by negative feedback, in the same way that in the mechanical world the motions of pendulums and springs are governed by gravity and elasticity. A profitable line of theoretical attack has exploited and developed this analogy (May *et al.* 1974). One of the salient results of these analyses is the insight that stability, over-compensation, under-compensation and so on all depend critically on the slope of the density dependence of population growth rate at carrying capacity. This slope is referred to as the 'strength of density dependence' in the papers by Sæther & Engen (2002) and Lande *et al.* (2002). Lande *et al.* develop this idea and show how the 'total' density dependence in a life history can be calculated, using a time-scale measured in generations. It is shown with examples how this can be estimated from the sum of the autoregression coefficients.

Sæther & Engen (2002) consider the important question of whether population dynamics varies between organisms with different types of life history. They show that much of the variation in the ability of birds to grow from low density can be explained by position in the 'slow–fast continuum'. Populations of 'fast' species—those with large clutch sizes and mortality rates—grow faster at low density and are more vulnerable to environmental stochasticity effects than 'slow' species.

To what extent might density dependence operate in humans? Clearly a question of importance to all, since the mechanisms by which it operates could determine the quality of life of future generations. Surprisingly, the question has not been considered in human demography in recent years, even though Pearl & Reed's (1920) important paper on density dependence of population growth rate used the population of the United States 1870–1920 as their worked example. In an intriguing analysis of population growth rate, birth rate and density, Lutz & Qiang (2002) show that density dependence does appear to operate in man. How it operates is, of course, an extremely interesting question. It may be, as Lutz & Qiang suggest, that there is an important psychological and/or perceptual component, so that with the availability of birth control people plan their family sizes and lifestyles with regard to local norms of behaviour.

At this point we begin to widen the scope of the analyses to include mechanistic, reductionist approaches. In the simplest case, density achieves its effects simply by

Phil. Trans. R. Soc. Lond. B (2002) **357**, 1149–1151
DOI 10.1098/rstb.2002.1130

1149

resource competition—generally competition for food. Methods of analysis of the resultant relationships were developed in particular by G. Caughley (e.g. Caughley & Krebs 1983), and prior to and subsequent to his death in 1994 his work has much influenced the development of mammalian ecology, especially in Australia and New Zealand (see Bayliss & Choquenot 2002; Davis *et al.* 2002). Krebs here argues strongly in favour of such mechanistic reductionist analyses, backed with experiment wherever possible; some of his points are also developed by Sutherland & Norris (2002). Krebs (2002) makes ecologists using the density paradigm think very carefully about the assumptions underlying their analyses. Since measured values of population growth rate are specific to the environment in which they are measured, it follows that analyses of long-term datasets are of little value unless the environment has been constant or nearly so. He provides an example in which the relationship between population growth rate and population density appears to have changed with time, over decades, and other examples in which density-dependent relationships vary from one place to another.

Sinclair & Krebs (2002) present a number of important new approaches. Starting with the premise that food supply is the primary factor determining population growth rate in animal populations, they consider the complications introduced by varying predation, social interactions and stochastic disturbances. In a series of diagrams that will fascinate many ecologists they compare density-dependent relationships in contrasted environments. Typically the contrast is in the presence or absence of predators. In this way we begin to get a feel for how population growth rate depends jointly on the densities of the study animals and their predators.

Bayliss & Choquenot (2002) look in depth at how two important herbivorous marsupial populations are regulated: kangaroos and possums. These species are high profile and of conservation and commercial importance, but despite intensive work for many years, scientific knowledge has made only a limited contribution to their management until now. The authors suggest that future progress will be obtained by a marriage between density-dependent and mechanistic consumer-resource models. Davis *et al.* (2002) extend the argument by considering the effects of temporal variability in the food supply on herbivores' distribution and abundance.

Hudson *et al.* (2002) provide a comprehensive account of one of the great studies of cycling populations, the red grouse in England and Scotland. Major themes are why the populations cycle, why the cycle lengths vary between populations and why some populations are more stable than others. A feature of this work has been the inclusion of experiments that identify the mechanisms that affect productivity and population growth rate. Food quality appears to account for variations in the maximum population growth rate between areas. Year-to-year variations within areas are generated by the effects of parasites on the fecundity of the grouse, though interactions with other natural enemies and spacing behaviour are also important. Man, who maintains the population as a game bird, has a more limited effect.

Sutherland & Norris (2002) propose the application of a new principle to mechanistic analyses, obtained by adding

relevant features of an animal's behavioural ecology. Aware that evolution is an optimizing process selecting features adaptive to the environments in which organisms find themselves, behavioural ecologists pay special attention to models incorporating behaviours that are optimal within the constraints imposed by an animal's mechanical limitations, its imperfect knowledge of the environment and so on (Krebs & Davies 1993). Models of this kind have been particularly successful in predicting the ways that animals, especially birds, distribute themselves in patchy environments. The approach appears to solve one of the core problems—understanding the dependence of population growth rate on the environment in which the population lives. This might in turn open up the chance to make more secure generalizations between environments and, perhaps, between species. In this approach the relationship between population growth rate and density can be extracted from the analysis, but it does not have to be—the relationship is an epiphenomenon of the mechanistic understanding.

Clutton-Brock & Coulson (2002) also obtain a fairly complete reductionistic understanding of the factors governing population change without invoking population growth rate as an intervening variable. Studying sheep and deer on two small islands from which and to which there is no migration, they have tracked numbers in each age class, and shown how the vital rates of each age class are determined by extrinsic factors, such as weather, parasites and so on. Knowing population structure and the state of the extrinsic factors, successful prediction of the next year's population structure is possible. This is achieved directly using a population matrix approach, without explicit calculation of population growth rate.

Many of the contributors have interests in conservation and Forbes & Calow (2002) are interested in the ways in which we protect the environment against potentially harmful chemicals. In practice the ecological risks of toxic chemicals are most often assessed on the basis of their effects on survival, reproduction and somatic growth—but which vital rate is the most sensitive varies with species and chemical, and population growth rate analysis offers a more robust approach. They conclude that, given sufficient time and resources, population growth rate analysis should form the basis of ecological risk assessment.

Godfray & Rees (2002) remind us that there is an important analogy between population growth rate and Darwinian fitness, provide perspective on the whole subject area, and judiciously consider the ways ahead.

In conclusion, we would like to emphasize some points made by many contributors. Although population growth rate is an important summary parameter, it is specific to the time and place in which it is measured, and the same will be true of knowledge of the determinants of population growth rate. To generalize we have to have further mechanistic understanding, and this can only come through knowledge of the factors that affect the births and deaths of individuals. When environmental effects are understood at this level, it should become possible to use demography to build a reliable overall picture of how extrinsic and intrinsic factors contribute to population growth rate. As in all areas of science, model-based understanding needs to be checked by experimentation, even

though this is peculiarly difficult in population ecology because of the scale, time and effort involved.

The Discussion Meeting focused on population growth rate as a key variable in ecology. Population growth rate links together seemingly disparate areas of ecology—habitat ecology, population ecology, conservation ecology, ecotoxicology—and this allows us to see ecology as a unified whole. We hope it will inspire field ecologists to collect and analyse more data using the approaches presented here.

Richard M. Sibly[1]
Jim Hone[2]
Tim H. Clutton-Brock[3] *May 2002*
[1]*School of Animal and Microbial Sciences, University of Reading, PO Box 228, Reading RG6 6AJ, UK*
[2]*Applied Ecology Research Group, University of Canberra, Canberra ACT 2601, Australia*
[3]*Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 2EJ, UK*

REFERENCES

Bayliss, P. & Choquenot, D. 2002 The numerical response: rate of increase and food limitation in herbivores and predators. *Phil. Trans. R. Soc. Lond.* B **357**, 1233–1248. (DOI 10.1098/rstb.2002.1124.)

Caughley, G. & Krebs, C. J. 1983 Are big mammals simply little mammals writ large? *Oecologia* **59**, 7–17.

Clutton-Brock, T. H. & Coulson, T. 2002 Comparative ungulate dynamics: the devil is in the detail. *Phil. Trans. R. Soc. Lond.* B **357**, 1285–1298. (DOI 10.1098/rstb.2002.1128.)

Davis, S. A., Pech, R. P. & Catchpole, E. A. 2002 Populations in variable environments: the effect of variability in a species' primary resource. *Phil. Trans. R. Soc. Lond.* B **357**, 1249–1257. (DOI 10.1098/rstb.2002.1125.)

Forbes, V. E. & Calow, P. 2002 Population growth rate as a basis for ecological risk assessment of toxic chemicals. *Phil. Trans. R. Soc. Lond.* B **357**, 1299–1306. (DOI 10.1098/rstb.2002.1129.)

Godfray, H. C. J. & Rees, M. 2002 Population growth rates: issues and an application. *Phil. Trans. R. Soc. Lond.* B **357**, 1307–1319. (DOI 10.1098/rstb.2002.1131.)

Hone, J. & Sibly, R. M. 2002 Demographic, mechanistic and density-dependent determinants of population growth rate: a case study in an avian predator. *Phil. Trans. R. Soc. Lond.* B **357**, 1171–1177. (DOI 10.1098/rstb.2002.1118.)

Hudson, P. J., Dobson, A. P., Cattadori, I. M., Newborn, D., Haydon, D. T., Shaw, D. J., Benton, T. G. & Grenfell, B. T. 2002 Trophic interactions and population growth rates: describing patterns and identifying mechanisms. *Phil. Trans. R. Soc. Lond.* B **357**, 1259–1272. (DOI 10.1098/rstb.2002.1126.)

Krebs, C. J. 2002 Two complementary paradigms for analysing population dynamics. *Phil. Trans. R. Soc. Lond.* B **357**, 1211–1219. (DOI 10.1098/rstb.2002.1122.)

Krebs, J. R. & Davies, N. B. 1993 *An introduction to behavioural ecology*. Oxford: Blackwell Science.

Lande, R., Engen, S. & Sæther, B.-E. 2002 Estimating density dependence in time-series of age-structured populations. *Phil. Trans. R. Soc. Lond.* B **357**, 1179–1184. (DOI 10.1098/rstb.2002.1120.)

Lutz, W. & Qiang, R. 2002 Determinants of human population growth. *Phil. Trans. R. Soc. Lond.* B **357**, 1197–1210. (DOI 10.1098/rstb.2002.1121.)

May, R. M., Conway, G. R., Hassell, M. P. & Southwood, T. R. E. 1974 Time delays, density-dependence and single-species oscillations. *J. Anim. Ecol.* **43**, 747–770.

Pearl, R. & Reed, L. J. 1920 On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proc. Natl Acad. Sci USA* **6**, 275–280.

Sæther, B.-E. & Engen, S. 2002 Pattern of variation in avian population growth rates. *Phil. Trans. R. Soc. Lond.* B **357**, 1185–1195. (DOI 10.1098/rstb.2002.1119.)

Sibly, R. M. & Hone, J. 2002 Population growth rate and its determinants: an overview. *Phil. Trans. R. Soc. Lond.* B **357**, 1153–1170. (DOI 10.1098/rstb.2002.1117.)

Sinclair, A. R. E. & Krebs, C. J. 2002 Complex numerical responses to top-down and bottom-up processes in vertebrate populations. *Phil. Trans. R. Soc. Lond.* B **357**, 1221–1231. (DOI 10.1098/rstb.2002.1123.)

Sutherland, W. J. & Norris, K. 2002 Behavioural models of population growth rates: implications for conservation and prediction. *Phil. Trans. R. Soc. Lond.* B **357**, 1273–1284. (DOI 10.1098/rstb.2002.1127.)