Population growth rates: issues and an application

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Current issues in population dynamics are discussed in the context of The Royal Society Discussion Meeting 'Population growth rate: determining factors and role in population regulation'. In particular, different views on the centrality of population growth rates to the study of population dynamics and the role of experiments and theory are explored. Major themes emerging include the role of modern statistical techniques in bringing together experimental and theoretical studies, the importance of long-term experimentation and the need for ecology to have model systems, and the value of population growth rate as a means of understanding and predicting population change. The last point is illustrated by the application of a recently introduced technique, integral projection modelling, to study the population growth rate of a monocarpic perennial plant, its elasticities to different life-history components and the evolution of an evolutionarily stable strategy size at flowering.

Keywords: population dynamics; population regulation; integral projection; life history

1. INTRODUCTION

This paper consists of two parts: the first is a general discussion of population growth rates, the factors that determine them and their role in studies of population regulation; the second is a specific example of the calculation of a population growth rate and its use in an evolutionary ecological study. The first part is based on the summary talk given in The Royal Society Discussion Meeting from which the collected papers are assembled in this issue, but was also much influenced by an informal discussion meeting hosted by the Novartis Foundation that immediately followed the meeting at The Royal Society, and which was attended by most of the speakers as well as other population biologists (see the Acknowledgements). But though the strongly expressed views of many of the participants have often affected or determined what we have written, this is not an attempt at a consensus, and the blame for any muddle-headedness rests with us alone.

2. POPULATION GROWTH RATE AND POPULATION REGULATION

(a) *Population growth rate*

Is it justified to give the population growth rate such a central position in population biology? Is it not just one of a spectrum of useful concepts that permeate population dynamics, a particularly important one perhaps, but not deserving of so pivotal a role? We see several strong arguments supporting the importance of population growth rate, but with a number of caveats.

First, population growth rate is the central tool in population projection, the exercise in which data from contemporary studies are used to say what the potential growth rate of an organism's population is, assuming that present schedules of birth and death (and possibly immigration and emigration) remain unchanged. The father of population projection is surely Malthus (1798) who in his 'Essay on the principle of population' recognized the essential geometric nature of population growth, and that this inescapably meant that either what we might now call extrinsic and intrinsic population factors must come into play to limit population growth. In the simplest case of an unstructured population, population growth rate is easily calculated as the number of births minus deaths per unit time. When the population is structured by age, size or another variable, calculating population growth rate is more complex as normally it can only be expressed implicitly as the root of the Euler-Lotka or equivalent equation (Hone & Sibly 2002), but today with the ready availability of powerful personal computing this is no longer an obstacle to its easy use. There is presently a huge armoury of techniques that can be used to explore how population growth rate is influenced by age- or size-specific entries in the organism's life table, or by variables that determine jointly multiple entries (Caswell 2001), and these are used routinely in applied areas of ecology such as conservation (e.g. Seamans *et al.* 1999), pest management (e.g. Shea & Kelly 1998) and ecotoxicology (e.g. Forbes & Calow 2002). Although the theory was originally developed for deterministic populations, an equivalent stochastic body of theory is now available (Tuljapurkar 1990), though obviously its use is more hungry of data.

Second, population growth rate is often the most natural response variable for the statistical analysis of the factors influencing a species' population dynamics. In the density-independent case, Caswell (2001) and others have developed statistical tools to partition observed variability

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in population growth rate into components associated with different life table entries, a process called retrospective analysis, conceptually distinct though related to population projection. Most modern techniques used to search for density dependence are based on analysing how population growth rate varies with density (e.g. Lande *et al.* 2002), as are attempts to search for periodicity in time-series (Kendall *et al.* 1999) and more exotic dynamic behaviour such as chaos (Sugihara & May 1990; Hastings *et al.* 1993; Ellner & Turchin 1995).

Finally, population growth rate intimately links population dynamics and evolutionary biology. Exactly how this link operates depends upon which model of evolutionary change is assumed. It is clearest when evolution is viewed as the successive invasion of new traits into a resident population (Metz *et al.* 1992; Rand *et al.* 1994). The course of evolution depends upon whether a trait increases or decreases in frequency, which involves determining whether the population growth rate of the clan of individuals with the invading trait is positive or negative (here assuming a log scale) in an environment some of whose properties, particularly the nature of the density-dependent feedback, are set by the resident trait. If density dependence in the population operates through age-independent mortality then evolution will maximize population growth rate, but this is not a general result and depending on exactly how density dependence operates, a variety of other criteria will be maximized (Mylius & Diekmann 1995). This theory can be extended to take into account stochastically varying environments (Ellner 1985).

In the quantitative genetic model of evolutionary change, additive genetic variation in different traits is assumed always to be present and the progress of evolution is determined by the variance-covariance matrix representing this variation and a vector of selection gradients describing how different traits contribute to the organism's fitness (Lande 1982). In the simple case of frequency-independent selection, the element in the selection gradient vector corresponding to trait x can be interpreted as the change in logarithmic population growth rate ($\log \lambda$) brought about by a small change in the trait ($\partial \log \lambda / \partial x$) which is related but not identical to sensitivities ($\partial \lambda / \partial x$) and elasticities ($\partial \log \lambda / \partial \log x$) from classical population projection theory (Lande 1982; van Tienderen 2000). Here, population growth rate provides the mean fitness of a population. Again, it is possible to extend the theory to more complicated scenarios such as stochastic environments, and traits with frequency-dependent fitness (Lande 1982).

But study of population growth rate is not synonymous with population dynamics and there are circumstances where it is not the central focus of enquiry. Consider, for example, conservation biology where species viability plans and programmes are frequently used to predict extinction risks and as management tools to help recovery programmes. If the population growth rate of a current population is measured, and no account is taken of how density dependence may alter population growth rate as density changes, then simple population projections may be quite seriously misleading (e.g. Grant & Benton 1996; Sutherland & Norris 2002). A very rare species with a positive growth rate may be in far greater peril than

expected if density dependence acts at low population densities, while a similar species with a negative growth rate may be relatively easily conserved if above a population density threshold it begins to increase quite rapidly (as with an Allee effect). A population growth rate of zero may say little about the fate of a population if the species is at an equilibrium set by limited habitat extent. Mills *et al.* (1996) and Brook *et al.* (1997) provide examples from grizzly bears and the Lord Howe Island woodhen where the incorporation of density dependence has a major effect on population viability analysis (see also Sutherland & Norris 2002). Similar arguments can be made from other areas of applied ecology, and these indicate that while population growth rate is a critical component of population dynamics, it should not be divorced from other aspects of population change.

(b) *The role of models*

Population biology has always advanced on two fronts, theory and experimentation, but the relationship between the two aspects of the subject has not always been cordial. A common criticism by some experimental ecologists has been that many models are overly simplistic, are hard to apply to real situations, and ignore the temporal and spatial heterogeneity inescapably present outside the laboratory. Much of this criticism has arisen when strategic models have been misapplied or misinterpreted as tactical models. By strategic models we mean those that are designed to explore the ramifications of general questions in ecology, questions such as whether an interaction between a predator and a prey with discrete generations and a random search by the predator give rise to persistent population cycles. Such questions can be answered only by using the tools of mathematics, and provide general hypotheses that can then be tested experimentally. Tactical models however, are tailor made for particular systems and are designed to predict their fate. They are used extensively, for example, in pest management to predict exactly when a crop should be sprayed, in epidemiology to determine the proportion of the population that needs to be culled or vaccinated (Anderson & May 1979; Anderson *et al.* 1996) and in fisheries to determine the size of the harvest that maintains stocks (Clark 1985). Some models of this type are purely statistical using explanatory variables such as current population densities and weather to predict future population densities or other parameters using methods that incorporate no explicit biological processes. Others include detailed biological processes, often in the form of large simulation models that use abiotic inputs as driving variables (e.g. Gutierrez *et al.* 1993).

We maintain that both types of model, in their right place, have served the subject well. Study of very simple single-species models first showed the potential dynamic complexity of populations, and contributed materially to the discovery of chaos in dynamical systems. Strategic models have shown us that two identical species cannot coexist in a temporally and spatially constant environment, and the resulting studies of niche segregation, competition/colonization trade-offs, and coexistence in environments that vary in time both through biotic and abiotic agencies have enormously enriched community ecology. Simple models have also shown that parasites and

parasitoids may, but do not necessarily, regulate the densities of their host populations, and have stimulated a large experimental programme to discover whether real host–natural enemy systems possess these properties. Strategic models on the one hand are often poor at incorporating the biology of real animals and plants, and poor at making quantitative predictions that can be used to test their applicability in the field (Krebs 2002). Tactical models on the other hand, while often successfully predicting changes in density, frequently do so at the expense of generality or an understanding of underlying processes. Those based purely on statistical prediction make no pretence at this, while large simulation models are often too complicated to disentangle the factors driving dynamics.

The distinction between strategic and tactical models has never been absolute, and especially in fields such as epidemiology there have always been some models that bridge the two classes (Anderson & May 1991). Recently, this blurring has been accelerating, giving a real prospect of analytical theory that better serves field biologists. The two factors that we suspect are most responsible for these changes are the increasing use of modern statistical methods in population dynamics (e.g. Bjørnstad *et al.* 1998, 2001; Lande *et al.* 1998; Yao *et al.* 2000; Fromentin *et al.* 2001; Lingjaerde *et al.* 2001) and the readiness of ecologists to construct relatively complicated models appropriate to particular systems, but from which the classic models of population ecology can be derived as limiting cases. The latter greatly assists in understanding the dynamics of the full model. This evolution has been occurring in all areas of population biology, but we choose two examples from our own fields to illustrate these trends.

Parasitoids are insects that lay their eggs in the bodies of other insects, and their hosts are invariably killed as the larval parasitoid achieves maturity (Godfray 1994). They are abundant members of virtually all terrestrial ecosystems and can be a source of major mortality for their hosts. Entomologists have successfully controlled outbreak pests by introducing parasitoids into an area, thus demonstrating the potential for parasitoids to control their hosts, though the extent to which they are the prime factor regulating hosts in natural ecosystems is still not clear.

Traditionally, host–parasitoid dynamics have been modelled in two main ways. First through computer-intensive simulations, typically of hosts that are major agricultural pests, and often with the explicit aim of improving pest management rather than understanding the underlying biology (e.g. Gutierrez & Baumgartner 1984). The second way is based on the discrete-generation form of the Lotka–Volterra model and was initiated by Nicholson & Bailey (1935) and particularly developed by Hassell, May and colleagues in the 1970s and 1980s (reviewed by Hassell (2000)). The basic Nicholson and Bailey model, which assumes among other things random search by the parasitoid, shows divergent oscillations and extinction of one or both insects. This is caused by the parasitoid overexploiting the host which leads to the density of first the host and then the parasitoid crashing; the host recovers, and then so does the parasitoid, but with a lag that causes the next crash to be even more catastrophic, and so on until one party goes extinct. Strategic models have shown that for the interaction to persist there

must be some refuge for the host during periods of high parasitoid densities, and that this refuge may be an actual physical refuge, a fraction of the population that is genetically resistant to the parasitoid, or a fraction that escapes parasitism in time or in space. Examples of all these types of refuge have been identified in field systems, but these simple population models have not proved effective in describing real interactions in the field.

Murdoch *et al.* (1987) introduced a way of modelling host–parasitoid systems that facilitates the incorporation of considerable biological detail. Technically these are age-structured models, which assume demographic rates are constant within predefined stage classes, the assumption allowing the models to be phrased as delay-differential equations (alternative formulations have been explored by Hastings & Costantino (1987)). They have been called ‘models of intermediate complexity’ (Godfray & Waage 1991) as they lie between the simple strategic and the strategic complex models described above, but the critical point is that although they are frequently too complex to study fully analytically, the Lotka–Volterra, Nicholson–Bailey or other strategic models can be derived as limiting cases. The original application by Murdoch *et al.* (1987) was to understand the persistence of the interaction between the red scale pest of orange trees and its parasitoids. The unusual biology of the host meant that it was poorly described by classic host–parasitoid models that either assumed discrete generations or omitted developmental time-lags, and Murdoch *et al.* (1987) were able to show that host–parasitoid persistence was possible if certain life-history stages were both long-lived and resistant to the natural enemies.

These models also proved valuable in explaining why some hosts and their parasitoids in relatively aseasonal tropical environments show population cycles with a period approximately equal to one host generation (Godfray & Hassell 1989). Traditionally, the cycles had been explained by temporary synchronization of the host age structure by rare events such as droughts or hurricanes. However, age-structured host–parasitoid models suggested that synchronization would decay quite quickly, but also that persistent generation cycles could be maintained if the parasitoid generation time was approximately half that of the host. In this case the system has two time-delays, which interfere with each other causing the cycle (similar phenomena had been observed previously in electronics). More biologically, the persistence of the cycle can be explained by the fact that the majority of parasitoid eggs are laid at the peak of the host generation cycle giving rise to a burst of parasitoids when host densities are at a trough in density, so reinforcing the cycle.

The models just described are still relatively simple, but the approach can be extended to more complex systems where this is justified by our biological understanding of the interaction. For insect–natural enemy interactions, most of this work has involved laboratory systems (though see Rochat & Gutierrez (2001)). For example, Begon, Thompson, Sait and colleagues have conducted a long series of experiments with the Indian meal moth, *Plodia interpunctella*, a small insect whose larvae feed on bran and other stored products (Sait *et al.* 1994a,b, 1997; Begon *et al.* 1995, 1996a,b). The moth is attacked by a variety of natural enemies, including several parasitoids and a gran-

ulosis virus (a type of baculovirus). The interaction is particularly complex as the moth itself in single-species culture shows generation cycles which are caused by asymmetric and highly age-specific interactions between different age classes (Nisbet & Gurney 1983; Briggs *et al.* 2000). The parasitoid only attacks certain age classes, while depending on which stage the virus attacks it may cause death or the establishment of a sublethal infection that alters development time and adult fecundity. In experiments with the host, a parasitoid and a virus, Sait *et al.* (2000) found that the dynamics exhibited by the three species system depended on the order in which it was assembled, indicating alternative dynamic attractors. A stage-structured model constructed on the basis of a knowledge of the natural history of the interaction predicted dynamics similar to those observed in the laboratory, although analysis indicated not only a single stable dynamic attractor but also a dynamic repeller about which population trajectories might orbit for long periods of time as transients (Sait *et al.* 2000). A criticism of this approach is that the model construction and the identification of the important time-delays in the system are to a degree *ad hoc*. It is thus interesting that a statistical analysis of the data using modern time-series analysis (see below) identified the same number and magnitude of time-delays as had been assumed based on the natural history (Bjørnstad *et al.* 2001). The two analyses had been conducted separately, but increasingly we see model formulation and statistical analysis proceeding hand-in-hand, and a good example of this is the work on ungulate populations described in this issue (Grenfell *et al.* 1998; Coulson *et al.* 2001; Clutton-Brock & Coulson 2002). Other examples of the application of models of intermediate complexity to insect systems include those of Hastings & Costantino (1987) and Costantino *et al.* (1997).

Our second example comes from studies of plant population dynamics. Because higher plants are rooted to one spot, the classical Lotka–Volterra models of ecological competition provide only a limited understanding of how diverse plant communities may persist (Grubb 1977). There have been a number of different approaches to developing a more realistic theory of plant competition (e.g. Tilman 1994; Pacala *et al.* 1996a). Here, we describe an approach that involves building spatially-explicit models parameterized from field data. These models are complex and can only be solved numerically, but then simpler ‘models of models’ can be constructed to understand the underlying processes that determine their results.

Consider a community of annual plants on a sand dune or similar habitat. What maintains their diversity in such a simple habitat? Obviously one explanation is niche differentiation, but other processes such as a competition–coexistence trade-off might also be involved. The system can be studied by modelling how the growth of spatially localized plant individuals is influenced by the species composition of other plants growing in the immediate neighbourhood, and then by modelling how growth translates into changes in population growth rate. Using this approach on a large spatially structured dataset, Rees *et al.* (1996) were able to show that density-dependent processes within different species’ populations lead to stable dynamics and that interactions between species were weak. They attribute these weak interspecific interactions

to niche partitioning, spatial segregation and the rarity of competitive dominants (Rees *et al.* 1996). Detailed experimental studies, which manipulate the local species composition using seed sowing experiments, support this interpretation (Turnbull *et al.* 1999), as do the results of recent modelling studies (Levine & Rees 2002).

This detailed mechanistic approach has been taken by Pacala *et al.* (1996a) to study succession and coexistence in temperate mixed forests. Here, the statistical parameterization of the model involved studying the growth and survival of trees in different neighbourhoods. The purpose of the model is to extrapolate from measurable fine-scale and short-term interactions among individual trees to large-scale and long-term dynamics of forest communities. The model demonstrates the importance of initial abundances, which continue to affect community composition well into succession (for more than 300 years for some species), and provides a remarkably accurate description of successional dynamics in temperate mixed forests.

We finish this section by pointing to a few other current trends in population modelling that we think are also narrowing the gap between theory and experimental work. The explosion of interest in behavioural ecology in the 1970s and 1980s prompted the question of whether an explicit consideration of how natural selection acted on animal behaviour might help the parameterization of population models. The issue here is not whether the demographic parameters used by population biologists are influenced by natural selection—of course they are—but whether evolutionary ecology can give insights into how they might respond to changing conditions in a way that would be difficult to go out and measure in the field. Too often, a behavioural ecological study is glossed by the comment that it will aid understanding population dynamics when in fact the variation in fecundity or survival under discussion is so small it will be swamped by the typical variation in the parameter that is observed in the field (we do not exempt ourselves from this criticism!). This is especially true for those animals that experience large fluctuations in population densities.

Recent studies of bird populations have, however, shown how behavioural ecology can be a valuable tool for population dynamicists. A good example comes from habitat use in shore birds such as oystercatchers (Stillman *et al.* 2000, 2001; Durell *et al.* 2001) and godwits (Sutherland & Norris 2002). Here, the problem is to estimate quantities such as winter survival and condition at the beginning of the breeding season from how birds distribute themselves across estuaries and other habitats that consist of mosaics of patches that differ in quality for the birds. Behavioural ecological theory predicts that in the simplest case birds should distribute themselves according to the IFD (Smith & Fretwell 1974). At the IFD, all birds have equal fitness and no bird can improve its fitness by changing its location; in practice this means that good patches have many birds feeding together, and poorer patches fewer competitors. The theory can be made more sophisticated by assuming heterogeneity in competitive ability, both through exploitation and interference competition, and by assuming that food depletion by birds has a negative feedback on habitat quality. Given a knowledge of the availability of potential habitats and the density of

different types of bird, IFD theory can be used to predict how birds distribute themselves across the habitat and how their food intake influences their risk of mortality and their ultimate condition at the start of the breeding season. Behavioural ecological arguments have also proved valuable in understanding the dynamics of territorial birds and mammals in which optimum territory size, or the existence of territories at all, is influenced by population density (e.g. Lewis & Murray 1993).

A second recent trend is the increasing attention being paid to stochastic effects in population dynamics. Including stochastic effects in population models is of course not new and some of the most important results are quite old (Bartlett 1957; May 1974), but the last few years have seen a growth in interest in how demographic and parametric stochasticity can combine to influence the fate of populations. The need for better models in conservation biology has partly been responsible for this, while interestingly there has been a fruitful application of techniques from population genetics to ecological problems (Lande 1993, 1998; Lande *et al.* 1998). Many field workers are distrustful of deterministic models that predict rigid, stable equilibria—'figments of modellers' imagination' as one speaker at the meeting described them—and while it is true that strict deterministic equilibria are hardly if ever observed in the wild, the stochastic analogue of these equilibria are much more realistic. Turchin (2001) describes an equilibrium as a probability distribution of densities towards which a population tends to return if disturbed, and this idea implicitly underlies many of the models of Australian vertebrate populations described at this meeting by Bayliss & Choquenot (2002) and Davis *et al.* (2002). The latter study in particular explored how observed variation in rainfall might affect mammal densities in two or three trophic level systems, while Bayliss & Choquenot (2002) and Sinclair & Krebs (2002) argued that many mammal populations exhibited alternative stochastic equilibria. But many organisms do exhibit dynamics that never approach an equilibrium (a number that is probably increasing as global change accelerates) and these must be studied using non-equilibrium approaches.

Finally, we mention briefly the huge growth in spatial modelling that has occurred in the last decade. Partly fuelled by the enormous expansion in desktop computing power, a large array of new techniques have been developed to study spatiotemporal population processes (excellently summarized by Dieckmann *et al.* (2000)). At present, theory far outstrips data, as is natural in a new field (though see Lande *et al.* (1999) for an example of a complex model that gives simple testable predictions). Perhaps ironically, the greatest progress in parameterizing spatial models has come in plant ecology (Pacala & Silander 1990; Cain *et al.* 1995; Pacala *et al.* 1996b). Early ecological theory was seldom applied to plants because of their sedentariness, but this same immobility both makes spatial effects more important and makes it easier to parameterize spatially explicit models. In animal ecology, the most important body of spatial theory to emerge concerns metapopulations, the dynamics of ensembles of populations loosely coupled by dispersal (Hanski 1999). A number of metapopulations are now emerging as model systems, in particular the butterfly *Melitaea cinxia* in the

Åland islands of Finland. Using a combination of modelling and experimentation, Hanski's group has shown, among other things, the existence of threshold conditions for the persistence of the metapopulation, as well as how inbreeding depression may be involved in population extinction (reviewed in Hanski 1999).

(c) *Observation and experimentation*

Since the days of Charles Elton's analysis of cycles in the numbers of lynxes trapped for their fur, population ecologists have studied time-series. Their two main goals have been the discovery of cycles and more complex dynamic behaviour, and the identification and measurement of negative feedback on population growth (density dependence). Traditional time-series techniques such as spectral analysis and autocorrelation are valuable for identifying significant cycles and their periodicity, but are limited in the extent to which they can be used to detect chaotic dynamics. Schaffer (1985) spearheaded a move to use model-free techniques to reconstruct dynamic attractors from time-series data, and then to look directly for the signature of chaos in the shape of the attractor, although it is now clear that these methods require too much data for most biological applications (Hastings *et al.* 1993). The first attempts to look for data in time-series involved fitting simple population models to data and then examining the model's dynamics (Hassell *et al.* 1976). Today, a direct descendent of this approach is most often used to search for chaos, but now a very flexible model in time-lagged population densities is fitted to population growth rates using response surface, splines or neural net techniques (Ellner & Turchin 1995).

Population ecologists in the 1950s debated vigorously whether populations were regulated by density-dependent or density-independent processes, and although the debate has subsided (and much of the disagreement was largely due to semantic confusion), there is still considerable interest in trying to measure the effects of direct and delayed density dependence on animal and plant populations. A series of statistical techniques of increasing complexity have been developed, although no single method is superior in all situations. Detecting delayed density dependence is particularly difficult, and Lande *et al.* (2002) show how in age-structured populations it is important to disentangle how delayed density dependence operates through the organism's life history to determine current population growth rates.

Krebs (2002) characterizes this approach to studying populations as the density paradigm which he contrasts with the mechanistic paradigm which seeks to identify the effects influencing population densities. The mechanistic approach dates back to key-factor analysis pioneered by ecological entomologists (Varley *et al.* 1973). The relationship between the two approaches is complex, but frequently the former is used in preliminary analysis when no other data are available, and if successful, for example in identifying significant population feedbacks, it may be very valuable in determining on which potential mechanisms to concentrate.

Probably all population ecologists would follow the mechanistic paradigm if they could, but one of the problems has been to integrate potential explanatory variables with the organism's life history into analyses of time-series.

Traditional techniques have problems incorporating both nonlinear terms and complex error structures. Recently, a series of new techniques, which incorporate mechanistic details of the organism's population biology, have been introduced to population ecology (e.g. Ellner *et al.* 1997, 1998; Turchin & Hanski 1997; Bjørnstad *et al.* 1998, 2001; Rees *et al.* 2002). These techniques allow stronger inferences to be made because they incorporate more information, and often outperform classical time-series methods. This approach when combined with recent developments in the statistical analysis of partially specified models (Wood 2001), where constraints on the properties of the functions fitted are imposed rather than assuming *a priori* functional forms, holds considerable promise. However, in the presence of temporally correlated (coloured) noise there may be real limits to the degree to which population mechanisms can be diagnosed from time-series data (Lundberg *et al.* 2000; Ranta *et al.* 2000; Kaitala & Ranta 2001; Jonzén *et al.* 2002). A different approach to introducing mechanism more explicitly into theoretical population dynamics is to produce models based on explicitly physiological processes. These models may be quite complex but offer the possibility of introducing new insights into such issues as how body size and other parameters influence population dynamics (Nisbet *et al.* 2000).

One goal of observational studies of time-series and other population data is to discover cross-species patterns in population processes. Silvertown *et al.* (1996) were one of the first groups to do this, comparing woody and herbaceous perennials and which elements of a population projection matrix had the greatest effect on population growth rates. Sæther and colleagues (Sæther & Bakke 2000; Lande *et al.* 2002) have used bird demographic data to show how fecundity and survival influence population growth rate and how these effects are correlated with other aspects of the bird's life history. In analyses of this kind it is important to consider statistical non-independence among species arising through phylogeny, and to control for this using modern comparative methods (Harvey & Pagel 1991). Population dynamics has always been important in life-history theory; for example, the theory of *r* and *K* selection, in its original sense, is a hypothesis about how a population dynamic constraint will influence life-history theory. But whereas large datasets on life-history characters are relatively easy to construct, data on population dynamics, with the possible exception of mean population size, are much harder to collect. Charnov (1993) was able to identify a series of life-history invariants—dimensionless combinations of life-history parameters—in a study in which he essentially assumed populations were perfectly regulated. As more comparative population data become available, it will be interesting to see if deviations from the patterns identified by Charnov are correlated with patterns in the dynamics.

While observational studies are invaluable in generating hypotheses about population processes and may be the only means of investigating processes that involve evolutionary time-scales, experimental studies, particularly in the field, are still the gold standard for testing specific hypotheses about population processes. For example, red grouse populations show cyclic behaviour on British moorlands. Because they are an economically important

game bird, long time-series of bag sizes are available and there is considerable information about their biology. As Hudson *et al.* (2002) describe in more detail, there are two hypotheses to explain the cycles, (i) that it is due to the interaction between the grouse and its main parasite, a nematode worm, and (ii) that it is due to intrinsic variation in grouse behaviour and quality over the course of the cycle. To test the first hypothesis, Hudson *et al.* (1998) carried out a large experiment in which they applied anti-helminthic drugs to four populations of birds just before an expected crash in population densities. Treated populations either did not decline in density, or the drop was much less than controls, strongly implicating parasites as a cause of the population cycle. But other field experiments also indicate that intrinsic factors may be involved. It is possible to manipulate grouse behaviour using testosterone implants and this influences territory size and survival (Moss *et al.* 1994). These are individual-level rather than the population-level experiments, but indicate how field experiments may be used to distinguish between different hypotheses (Fox & Hudson 2001).

This example illustrates the value of large-scale experimental studies but also the huge investment in time and resources needed to carry them out properly, and these are by no means the largest field experiments in population ecology. Tilman (1993, 1994, 1996, 1997) has set up a large series of experiments at Cedar Creek in Minnesota designed to test a wide range of hypotheses about the mechanisms of plant coexistence and the relationship between community and ecosystem processes. These experiments involve manipulating and maintaining community composition in thousands of experimental plots, and the results obtained have become clearer and easier to interpret the longer the experiment has run, illustrating the value of long-term studies. The Kluane experiment in northern Canada designed by Krebs *et al.* (2001) as a factorial experiment to test how predation and food supply influence snowshoe hare dynamics was so ambitious that the relevant research council had to invent new procedures to deal with it.

Population ecology is by no means unique in requiring large experiments, and in fact our most grandiose schemes are paltry compared with the costs of a new particle accelerator. But the particular problem faced by ecologists is the diffuseness of the subject and the difficulty the community has in agreeing on model systems that can attract cross-community support for major investment. There is a trade-off between concentrating large amounts of resources to get a more accurate answer to one particular question, and dispersing resources more widely to get more approximate answers to a wider range of questions. Deciding the optimum resource allocation is difficult without knowing how the results from one system generalize to all systems, an issue about which there is little consensus in the field. A related question is the degree to which systems of applied relevance—invasive species, fisheries and timber trees—for which funding for long-term research is easier to obtain, give us answers to general problems in the subject. Where ecology does differ from most other experimental sciences is in its need for long-term experiments, their duration often set by the lifespan of the study organism that may be of the same order of magnitude as the lifespan of the experimenter. Thus, a

further argument for establishing model systems is to break the tie between the length of a study and the length of an ecological career.

An issue on which it is perhaps easier to agree is the need to improve accessibility to long-term population data, both observational and experimental. Some schemes do already exist, for example the GPDD (<http://cpbnts1.bio.ic.ac.uk/gpdd/>) administered by the NERC Centre for Population Biology in the UK which contains 5000 time-series of greater than 10 generations in length. Except where the organizations providing the data imposed conditions, these data are freely available to the community for study. However, the data in the GPDD are relatively simple, in the sense that they consist of raw time-series data with little annotation, with none of the ancillary material generated by detailed field studies and experimentation. Creating a true data repository of the types now available in molecular biology would require the development of means of making data portable, and accessible across different platforms. Recent advances in metadata formats that are beginning to be applied to ecological data may help to provide a solution to this (<http://knb.ecoinformatics.org/>). A further issue is the degree to which individual workers should be asked to make data available to the community. Much population data are so hard to obtain that it seems only fair that the investigator has a 'fair crack of the whip' before it is made generally available, but there is need for the community to agree on equitable rules on data sharing.

Our discussion of experiments has focused on field studies, but what is the role of laboratory experiments in studies of population, of growth rate and population regulation? One view is that they are too divorced from reality to say anything cogent about processes operating in the field, an opinion perhaps most often put forward by people working on larger organisms whose size and complex behaviour make them poor laboratory models. But we tend to agree more with Kareiva (1989) who argued that 'ecologists gave up bottle experiments too soon'. We mentioned above a series of experiments using insects pests of stored products and their natural enemies, and we argue that these provided valuable insight into how age-structured interactions may lead to different types of population cycling. Using a similar system, Bonsall & Hassell (1997) were able to show how one species may drive another to extinction when their only contact is a shared natural enemy, something long predicted by theory but which has proved difficult to study in the field. Much more complex laboratory communities can be assembled using micro-organisms. For example, using communities of protists, Kaunzinger & Morin (1998) found that more enriched habitats can support longer food chains, as predicted by classical theory. However, both higher enrichment and longer food chains are thought to be destabilizing, indicating dynamic constraints on food chain length. Protist microcosm experiments also first demonstrated the destabilizing effects of enrichment (Luckinbill 1973) and increasing food chain length (Lawler & Morin 1993). Theory predicts that metapopulation dynamics might stabilize otherwise-unstable predator-prey interactions, a prediction first confirmed in replicated experiments by Holyoak & Lawler (1996). At their worst, laboratory experiments are so artificial that

they are merely analogue computers solving the problem set by the investigator, but at their best they can test between novel hypotheses and aid both further theory and the design of experiments on more natural systems in the field.

Finally, we ask to what degree individual species or groups of closely interacting species can be treated in isolation. Do the majority of species in natural systems interact with so many other species that considering them in isolation is doomed to failure? Does this underlie some of the problems with the repeatability of studies highlighted by Krebs (2002)? These questions are easier to pose than to answer, or to think about how experiments could be designed to address them. However, this is an area where plant ecologists are probably leading the way in developing a quantitative community ecology. We have already discussed how spatial models of plant communities have been constructed and parameterized, and then used to investigate questions of community succession and coexistence. Another large plant community project is the network of 50 ha plots set up by the Centre for Tropical Forest Science at the Smithsonian Tropical Research Institute in which all trees above 1 cm diameter are censused at regular intervals. The original 50 ha plot was set up on Barro Colorado Island in Panama, but there is now a network of six or so large plots and others that are slightly smaller in all the major regions of tropical forest of the world (<http://www.ctfs.si.edu/>). This project in population ecology perhaps comes nearest to the mega-projects of particle physicists and astronomers, and has already been used to explore global patterns in rainforest diversity, the role of Janzen-Connell effects in maintaining diversity, and to study the comparative demography of trees (Condit *et al.* 2000). It has also stimulated radical new theory (Hubbell 2001). Though not experimental, we suspect that such projects may be our best hope of understanding the dynamics of complex, long-lived communities.

3. INTEGRAL PROJECTION MODELS

In this second part of the paper we switch from a general discussion of issues in population dynamics to a much more specific application of population growth rate to a problem in plant population and evolutionary ecology. This application does, though, illustrate some of the themes of the preceding section: the value of population growth rate and population projection, the constant flow of new techniques into the field, and the intimate link between population dynamics and evolution.

Population projection has been widely used in plant ecology and has largely been based upon matrix models in which individuals are either classified by age or size (Caswell 2001). This works well when the classes are discrete and easily recognized, but can lead to problems when what is essentially a continuous distribution in a variable such as size is cut up into discrete stages. Algorithms exist to help choose the optimal partition of the size distribution (e.g. Vandermeer 1978), but these cannot eliminate the essentially arbitrary nature of the division, and the problem that the number of classes chosen may influence the apparent relative importance of different biological processes (Enright *et al.* 1995).

To help solve these problems, Easterling *et al.* (2000) introduced integral projection models that retain many of the analytical advantages of traditional matrix models but which avoid the need to specify arbitrary distinct stage classes. As an example, they apply the technique to a herbaceous perennial, *Aconitum noveboracense* (northern monkshood), which reproduces by a mixture of sexual and vegetative means, calculating population growth rate and the elasticities and sensitivities to different size classes. Here, we briefly describe integral projection models and how they might be applied to a plant with a different life history, the monocarpic large-flowered evening primrose *Oenothera glazioviana*, and used to answer questions in evolutionary as well as population ecology. For further details of integral projection techniques see Easterling *et al.* (2000) and for its application to *Oenothera* see Rees & Rose (2002).

(a) The technique

In matrix projection, a vector $\mathbf{n}_t$ representing the numbers or densities of individuals in different stage classes at time t is acted upon by a transition matrix $\mathbf{K}$ to predict the numbers in the different stage classes at the next time-step, $\mathbf{n}_{t+1}$. In symbols

$$\mathbf{n}_{t+1} = \mathbf{K}\mathbf{n}_t \quad (3.1)$$

The transition matrix contains terms representing stage-specific fecundity and survival. The structure of an integral projection model is very similar except now the vector is replaced by a function representing the numbers or densities of individuals in stage y at time t , $n(y, t)$. For narrative simplicity we will henceforth view y as plant size. As with matrix models, time is treated as discrete and we can calculate the distribution of individuals in different size classes at the next census point using

$$n(y, t+1) = \int k(y, x)n(x, t)dx \quad (3.2)$$

Here $k(y, x)$, the kernel function, describes the number of transitions between an individual in size class x at time t and size class y at time $t+1$. A transition might occur through growth or through sexual or vegetation reproduction. Biologically, it is useful to distinguish between these two processes,

$$k(y, x) = p(y, x) + f(y, x), \quad (3.3)$$

where $p(y, x)$ is the survival-growth function, the probability that an individual size x survives and grows (or conceivably shrinks) to size y (a plant that remained the same size would contribute to a self-transition or $p(x, x)$ term); and $f(y, x)$ is the fecundity function, the number of offspring that are sized y at the next census that are produced by a plant currently of size x .

For the matrix case (equation (3.1)), classical mathematical results prove that if $\mathbf{K}$ is a time-invariant matrix, the population will come to grow (or decline) at a rate λ that is independent of the initial values of the population vector (Caswell 2001). The population growth rate, λ , is the dominant eigenvalue associated with $\mathbf{K}$, while the right and left eigenvectors represent respectively the stable stage distribution and the vector of the Fisherian reproductive values associated with each stage class. Exactly equivalent

quantities can be calculated for the integral projection matrix; λ as before is a simple scalar while the eigenvectors are replaced by functions that describe the distribution of individuals of different size ($w(y)$) and how reproductive value changes with size ($v(y)$). Much of the complex machinery described by Caswell (2001) for matrix models translates to the integral projection case, but here we highlight just one example, elasticity. As mentioned earlier, the elasticity ($e(y, x)$) is the proportional change in population growth rate consequent on a proportional change in one element (y, x) of the transition matrix or, in this case, of the kernel

$$e(y, x) = \frac{\partial \log \lambda}{\partial \log k(y, x)} = \frac{k(y, x)}{\lambda} \frac{\partial \lambda}{\partial k(y, x)} = \frac{k(y, x)}{\lambda} \frac{v(y)w(x)}{\langle v, w \rangle}, \quad (3.4)$$

where $\langle v, w \rangle = \int v(x)w(x)dx$ and is a normalizing constant. The elasticity can be understood intuitively as proportional to the product of the size of the size class from which the transition occurs ($w(x)$) and the importance of the size class to which the transition occurs ($v(y)$).

(b) The dynamics of *Oenothera glazioviana*

The kernel can be decomposed further beyond $k(y, x) = p(y, x) + f(y, x)$ as the biology of the system dictates. With *O. glazioviana* we have extensive knowledge of its population ecology thanks to the work of Kachi (1983) and Kachi & Hirose (1985). In their sand dune study site, *O. glazioviana* exists as rosettes of varying size which survive from year to year (t is measured in years) until they flower which is always followed by the plant's death. Based on their work, fecundity can be expressed as a product of three functions

$$f(y, x) = p_f(x)f_n(x)f_d(y, x), \quad (3.5)$$

each of which can be statistically estimated from data (Kachi & Hirose 1985). $p_f(x)$ is the probability that a plant of size x flowers in the current year and was estimated as a logistic function of x . $f_n(x)$ is the fecundity of plants of different size and it was found that the logarithm of seed number was linear in x . Finally, $f_d(y, x)$ is the size distribution of recruits. Data were not available on the size of recruits derived from seeds of plants of different size, but evidence from other systems indicates a low maternal effect on recruit size (Weiner *et al.* 1997), and this function was estimated as normal on a logarithmic scale, independent of x .

The growth and survival function was also treated as the product of three functions

$$p(y, x) = (1 - p_f(x))s(x)g(y, x). \quad (3.6)$$

As flowering always results in the plant's death, growth and survival are contingent on *not* flowering, which is given by the first term. The second term, $s(x)$, is the size-specific probability of flowering which was well estimated by a simple linear term. Finally $g(y, x)$ is the probability of growing from size x to size y which was estimated as a normal distribution with fixed variance and the mean a linear function of rosette size.

Putting all this together we can estimate the shape of the kernel, $k(y, x)$ (figure 1) and based on this we can calculate $\lambda = 1.041$. Unfortunately, we do not have field

Figure 1. The shape of the kernel function $k(y, x)$ for *Oenothera glazioviana*: the number of transitions between an individual in size class x at time t and size class y at time $t + 1$.

Figure 2. A comparison between the stable size distribution predicted by the integral projection model (curve) and a detailed IBM developed by Kachi & Hirose (1985).

estimates of λ with which to make a direct test, but we can compare this result and the predicted stable size class distribution with the output of a detailed IBM described in Kachi & Hirose (1985). The IBM predicted $\lambda = 1.04$ and the stable stage distribution was accurately described by the integral projection model (figure 2). We conclude that the integral projection model captures the same detail of the biology as the IBM, but in much more concise and analysable form.

Finally, in this section, we calculate the elasticity surface (figure 3). As indicated in the figure, the most important determinants of population growth rate correspond to, in decreasing order, the fecundity of large plants, the growth of plants into the chief flowering category and the growth of younger plants.

Figure 3. The elasticity of population growth rate to variation in the transition kernel. The biological interpretation of the different peaks is indicated.

(c) The evolution of size at flowering

One of the most critical life-history decisions of a monocarpic plant such as *O. glazioviana* is the size at which to flower. We can extend the integral project model to analyse this question, but first we have to be explicit about exactly where density dependence operates. The available evidence indicates that density dependence acts purely on seedling establishment with no later intraspecific competition (Kachi & Hirose 1985; Rees *et al.* 2000), in which case evolution maximizes R_0 , total lifetime reproduction (Mylius & Diekmann 1995). If the population was at demographic equilibrium with flowering strategy $p_f(x)$ we could then explore whether any alternative flowering strategy, $\hat{p}_f(x)$, was able to invade. In fact the population is slightly increasing ($\lambda = 1.041$) and so we reduced the probability of seedling establishment slightly so that $\lambda = 1$ for the resident strategy.

We modelled the probability of flowering as a logistic function of plant size

$$\text{logit} p_f(x) = a + bx, \quad (3.7)$$

which indicates that flowering size is determined by the two parameters a and b . This formulation, while statistically well-grounded, is biologically rather difficult to interpret as the mean and variance of the size at flowering are both functions of a and b . In Appendix A we show how these can be disentangled and in figure 4 show the fitness (population growth rate) of flowering strategies that differ from the resident in mean size and variance in the size at flowering. The results show clearly that the current mean size at flowering is an ESS, though it does indicate that natural selection should act to reduce the variance in size at flowering. This selection for a threshold size at flowering is expected from general models of evolution in a constant environment (Sasaki & Ellner 1995).

There are at least two possible explanations for the variance in flowering time not being an ESS. First, the variance may be a constraint, either genetic or phenotypic, that prevents the plant from evolving more of a threshold response. However, studies of the monocarpic species, *Cynoglossum officinale*, have demonstrated sharp threshold flowering strategies are possible (Wesselingh *et al.* 1993). A similar analysis of another monocarpic plant, *Carlina vulgaris* suggests an alternative explanation (Rose *et al.* 2002). In this study an IBM model was used to study the invasion of alternative flowering strategies. When the

Figure 4. The fitness of alternative flowering strategies when invading a population with the observed phenotype in the field (shown by a black disk). As explained further in the text, the flowering strategy can be characterized by the mean size of flowering (on the x -axis) and the variance around this mean. No strategy with a different mean can invade, but the analysis indicates that strategies with lower variance have higher fitness.

equivalent of a time-invariant matrix or kernel was assumed, the observed mean size at flowering was larger than the predicted ESS and no variance was predicted. However, in that study, data were also available on the temporal variance in life-history parameters and when these were included in the IBM non-zero variance was predicted (Rose *et al.* 2002); in a variable environment, some degree of spreading of risk is selected (Sasaki & Ellner 1995). We conjecture that were data available on temporal variance in the parameters of *Oenothera* life history, some degree of variance in size at flowering would be selected. Extending integral projection techniques to encompass temporal variance in parameters, as has been done for projection matrices (Caswell 2001), would be a useful future step.

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APPENDIX A

In this appendix we show how the fitted parameters of a logistic regression can be interpreted in terms of an underlying, unobserved distribution of threshold sizes for reproduction. Assume there is some distribution of threshold sizes for flowering within a population; then for a particular size, x , if 50% of plants flower, this implies that 50% of the population have a threshold less than x (Wesselingh & de Jong 1995). In this way we may inter-

pret the fitted logistic curve as a cumulative distribution function; hence, differentiating equation (3.7) gives the probability density function of threshold sizes for reproduction within a population. Calculating $\partial p_f(x)/\partial x$ we obtain

$$f(x) = \frac{b \exp(a + bx)}{(1 + \exp(a + bx))^2}, \quad (\text{A } 1)$$

which defines a general logistic distribution with scale parameter $1/b$ and location parameter $-a/b$. This distribution has mean and variance given by

$$\mu = -a/b, \quad (\text{A } 2)$$

and

$$\sigma^2 = \frac{\pi^2}{3b^2}. \quad (\text{A } 3)$$

In this way, we may express the distribution of threshold sizes within a population in terms of the estimated parameters of the logistic flowering function (equation (3.7)). There are problems applying this approach to real systems, as there is growth between the time flowering decisions are made and flowering occurs. However, the approach is still useful for interpreting model parameters.

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GLOSSARY

- ESS: evolutionarily stable strategy
 GPDD: global population dynamics database
 IBM: individual-based model
 IFD: ideal free distribution