

2. Current Paradigms of Rodent Population Dynamics — What Are We Missing?

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Abstract

Rodent population studies have played a key role in developing our understanding of population dynamics. The proximal stimulus to this understanding is to alleviate problems of rodent pests in agriculture and disease transmission to humans.

Ideas about rodent population dynamics have gone through three phases. In the 1930s there were almost no quantitative data, and population control was believed to be caused by biotic agents that operated in a density-dependent manner. By the 1950s a new paradigm of social control of numbers emerged with emphasis on physiological stress and social aggression within populations. By the 1970s a synthesis of sorts had emerged suggesting that multiple factors caused population changes. Experimental manipulation of field populations in the 1960s enlarged our outlook on the complexities of rodent populations, and the emergence of modelling and rigorous statistical analyses of survival and reproduction in the 1980s and 1990s has shown again that rodents have been *Drosophila* of population ecology. But as precision has increased over time, generality and simplicity have declined to near extinction.

What is missing and what do we need to do in the next 20 years? Experimentation is the key to understanding, and no study should be undertaken without a clear set of experimental predictions. The era of alpha-level descriptive population studies should be over. We need large-scale, extensive studies coupled with short-term experimental studies. Rodents are good candidates for studies of spatial dynamics, a strongly emerging subdiscipline in ecology. Also, rodent management should focus on the factors limiting populations and use an experimental approach. The era of pest eradication via killing alone should be over and we need to be smarter in developing our management options. The development of genetic resistance to anticoagulants and chemical poisons is a call to the ecologists of the 21st century to think more clearly about how we might outwit rodent pests. The accumulated knowledge of the physiology, behaviour, and genetics of rodents needs to be integrated into our management options. There is much to be done both to understand and to outsmart these clever mammals.

Keywords

Population regulation, population limitation, food, predation, social behaviour, rodents, pest management

INTRODUCTION

POPULATION DYNAMICS is without question the most highly developed of the subdisciplines of ecology. From abstract mathematical models to field experiments, ecologists have made progress over the last 50 years in analysing population changes in many species. In particular, rodents have been model organisms for studies of population dynamics for three reasons. First, they are conveniently short-lived so that a scientist or a postgraduate student can accomplish something within the constraints of a 3–4 year time window. Second, they are ubiquitous, occur in abundance nearly everywhere, and are relatively cheap to study, and are often of economic importance (Singleton et al., Chapter 1). Third, they do interesting things such as have population outbreaks that occur frequently enough that even politicians think that something must be done about them, at least when they are superabundant. All these features have combined to produce a very large literature on rodent population dynamics that is somewhat overwhelming to the novice. It is important therefore to step back and ask what we have accomplished with these studies, how useful it has been for pest control, and what is to be done next. This book brings together ecologists, physiologists, and ethologists with a common interest in rodent biology and thus provides an ideal time to address these larger issues for rodents.

After a historical overview I will summarise the three current paradigms of rodent population dynamics, assess their

strengths and weaknesses, and suggest some paths for future growth.

WHAT ARE THE PROBLEMS?

Ecological questions are complex and one thing we have learned is to ask very specific questions about populations so that we can answer them clearly. Three major questions have formed the focus of population dynamics (Krebs 1994, p. 322; Krebs 1995):

- ▶ What stops population growth?
- ▶ What limits average abundance?
- ▶ What constrains geographical distributions?

To find out what stops population growth, we must compare a growing population to one that is not growing, and the usual approach is to look for some factors causing negative feedback in the form of density dependence. The second question is very broad and is answered by the use of the comparative approach in which a high-density population is compared with a low-density population to see what factors are associated with the observed differences in density. In both these cases an experimental approach is useful to answering the question most quickly and avoiding spurious correlations (Underwood 1997).

Most academic rodent ecologists have addressed the first question—the problem of regulation (Berryman 1986; Sinclair 1989), and this has engendered much discussion about density dependence in natural populations. Fewer ecologists have worked on the second question—limitation of numbers, and yet this is the critical question for pest management. In a simple world, the

same ecological factors would limit and regulate a population, but this has never been found in the real world. Limitation often comes from habitat factors that students of regulation seldom consider, as we shall see. In a sense these two aspects of population dynamics correspond to the two statistical concepts of the mean and the variance of a set of measurements. We shall be repeating history to complain, as do many statisticians, that scientists are often preoccupied with the mean and tend to forget about the variance.

The question of what constrains geographic distributions has fallen out of favour until fairly recently when the consequences of global warming on north–south geographical distribution boundaries became a hot topic of worry. It is an important issue that I cannot deal with here, and there has been much discussion of the consequences of these biological invasions (Ehrlich 1989; Ruesink et al. 1995; Vitousek et al. 1996).

HISTORICAL OVERVIEW

Population dynamics has gone through three phases during the last 75 years. They have overlapped little in time but have phased into one another, with an abundance of outliers of the ‘flat-earth’ society type that bedevils ecology in general.

Phase I

The first phase began with the debate in the 1920s and 1930s about the role of biotic and abiotic factors in population regulation. The champions were A.J. Nicholson (1933) for the biotic school and a variety of opponents for the abiotic school (e.g. Thompson 1929;

Uvarov 1931). The winners were the Nicholsonians with their focus on regulation via density-dependent processes, in which the main agents were predators, parasites, diseases, and food shortage. The habitat was nowhere to be seen, and weather was noise for population dynamics. Most of this early discussion was about insect populations, and rodents were not a part of the discussions. This was an age of data-free ecology, and the arguments were typically theoretical in the bad sense of this word with no experiments on natural populations available. I have referred to the Nicholsonian world-view as the density-dependent paradigm (Krebs 1995).

It is important to remember that from the start all ecologists implicitly believed that a population can be identified, that community interactions are all direct and easily definable, and that population processes are repeatable in space and in time. These are three gigantic leaps of faith that came back later to challenge simplistic models.

Phase II

The second phase of population dynamics began in the 1940s when ecologists began to realise that social processes could affect births, deaths and movements. Among the leaders of this phase were David E. Davis and John Christian in the United States and Dennis Chitty in England (Christian 1950; Chitty 1952; Davis 1987). Rodents were the key to this new phase, which built partly on the earlier recognition by some ornithologists that territoriality could regulate the breeding density of some bird species. Attention turned in this phase to studying the physiological and behavioural

impacts of individuals on one another. One of the early striking experiments was done on rats in Baltimore by Davis and Christian (1956, 1958) who showed that one could reduce the population of rats in a city block by *adding* rats to the population (Figure 1), a completely counterintuitive result for the 1950s. Social strife for breeding space in rodents became a hot topic, and John Calhoun suggested crowded mice and rats as potential models for people in cities (Calhoun 1949). Much of this early work was done on house mice and rats in enclosures, and one of the dominant themes of criticism was that these enclosures were very high density, artificial environments and of little relevance to what went on in natural populations.

Social regulation of population size arose as an alternative explanation of population changes in populations that did not seem to

be regulated by the conventional Nicholsonian predators, parasites, or food shortages (Chitty 1960). These studies interfaced well with emerging work in ethology and behavioural ecology, which indicated the complex social structure of many mammal populations, and the interest population geneticists began to show in the dynamics of natural populations (Ford 1975). There was, among many ecologists, considerable scepticism that social processes, in contrast to the extrinsic factors of predators, food supplies and parasites, might explain changes in numbers. A series of elegant experiments on bird populations (e.g. Watson and Moss 1970; Moss and Watson 1980) helped to convince some sceptics, and parallel work on rodents (e.g. Krebs et al. 1969; Tamarin and Krebs 1969; Gaines and Krebs 1971) strongly supported the concept of social limitation of population density.

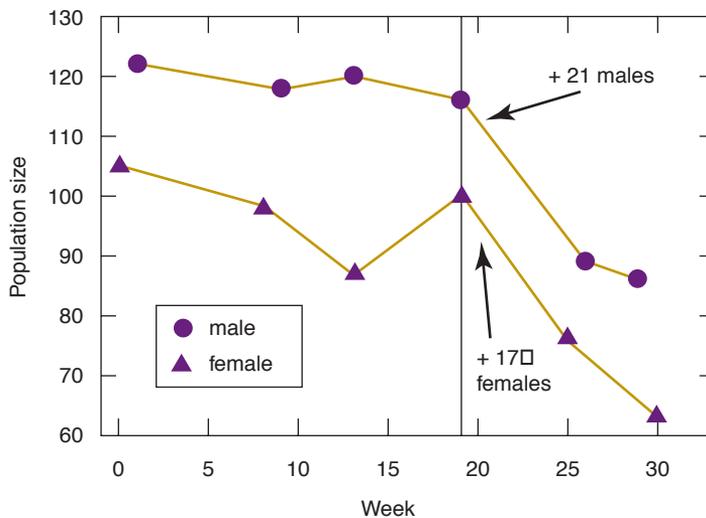


Figure 1.

Introduction experiments of Norway rats (*Rattus norvegicus*) into two city blocks in Baltimore in 1954.

Adding rats to a stationary population did not increase numbers but caused them to drop (after Davis and Christian 1956).

Phase III

By 1970 nearly all the ideas about population regulation and limitation were on the table for consideration and a synthesis began by suggesting that everyone might be correct, that multiple factors could be involved in both regulation and limitation (Lidicker 1973, 1988). Two developments accompanied this phase of population studies. First, experimental testing of hypotheses in field situations became the norm in ecology. Second, mathematical models began to be applied to specific questions about rodent systems in order to explore assumptions with rigour (e.g. Stenseth 1978, 1981b). The question then became how to articulate multiple factor hypotheses within the paradigm of experimental ecology. All ecologists are happy to conclude that the world is a complex multivariate system, but almost all agree that we must abstract from this complexity to some order to make progress.

Many multiple-factor hypotheses suffer from three deficiencies. Excessive complexity is the first lethal deficiency. A good example occurs with many flow chart models of population processes. Batzli (1992), for example, lists 22 hypotheses for rodent population cycles and gives a complex flow chart to illustrate some of the interrelationships involved. Limited predictability is a second problem with multiple-factor hypotheses. It does us no service to tell managers that we cannot predict anything about their potential pest problems because the world is complex. Third, many multiple-factor hypotheses are impossible to test experimentally. Without an experimental approach rodent ecology will make little progress.

The solution to these problems is fairly straightforward. We should encourage multifactor models of limited complexity, quantitative predictability, and feasible experimental tests. Note that there are two distinct types of multi-factor models of population limitation.

Several independent factors limit average abundance

The key point in this alternative is that the several factors that affect abundance are independent in a statistical sense. In practice this means hypothetically that if you change factor A and double numbers, and change factor B and triple numbers, you expect that if you change both factor A and factor B at the same time you will change numbers by the simple multiple (2×3) or 6 times.

Several interacting factors limit average abundance

This is the most complex alternative hypothesis since it postulates a statistical interaction between some factors. In practice you would recognise an interactive explanation by the fact that changing factor A and factor B at the same time does not result in their joint effect being predictable. In the above example, changing factor A and factor B might change numbers much less than 6 times, or much more than 6 times. If this hypothesis applies to your rodent population, interest centres on exactly how the ecological interaction of factor A and factor B operates mechanistically.

A straw poll among rodent ecologists would probably find most of them supporting multi-factor hypotheses of regulation and limitation. If this turns out to be the most frequent model for rodents, it

raises the multifactor dilemma that it is difficult to deal with more than three factors in any realistic model. There are two possible solutions to this dilemma. First, we can hope that all factors operate independently (hypothesis 1 above), so that if we have four or five significant factors for a particular herbivore, the factors do not interact. Second, we can hope that for systems with interactions only two or at most three factors show interactive effects (hypothesis 2).

The recent history of rodent population studies has been a history of reduced generality, increased precision, and decreased simplicity. Philosophers would be appalled at this, but ecologists should be happy to see us move away from superficial generality and simplicity. The touchstone of our progress must be the management of rodent pests, and we must try to answer this important question:

how much have our ivory tower studies of rodents in the laboratory and in the field helped us to solve problems of rodent pests?

THREE CURRENT PARADIGMS

There are three current paradigms that represent the dominant focus of work today on small rodent populations.

The food paradigm

The food paradigm states that both the quantity and the quality of food supplies regulate rodent population density. Food supplies also limit the average density of populations, and outbreaks of rodents are caused by changes in their food supplies. The most important thing you need to know, under this paradigm, is what do your

rodents eat and how much of it is out there in their habitat. These are themselves complex issues since diets change seasonally and may be affected by an individual's sex and age and also by changes in plant productivity from year to year and season to season. A test of the food paradigm is done most easily by supplementing food supplies artificially, although these experiments themselves can be called into question if the food given is not adequate nutritionally.

The food paradigm cannot be tested as a unit and needs to be applied to specific cases to make predictions that can be falsified. For example, the average abundance of a rodent pest might be higher where more food is available. Ecologists often pyramid hypotheses about food supplies. A recent example is the hypothesis about Lyme disease in eastern United States of America (Ostfeld 1997; Jones et al. 1998): food supplies in the form of acorns from oak trees are postulated to limit the average abundance of deer mice (*Peromyscus maniculatus*), trigger outbreaks of these mice (when acorn crops are heavy), and regulate density through starvation. Boutin (1990) concluded in his review of feeding experiments that, by adding food to terrestrial herbivore populations, one could increase density two to three-fold but not more, so that clearly for some populations food limits density over some restricted range only. Ecologists tend to despair when their favourite explanation does not apply to all species in all situations. We should be more modest in our aims. Food is clearly one of the dominant ecological factors limiting and regulating rodent populations, and the question is which populations and under exactly what conditions.

The predator paradigm

Many things eat rodents and some ecologists look to these trophic links to explain regulation and limitation of populations. The predator paradigm states that mortality caused by predation regulates rodent populations, that generalist predators limit the average density of populations below the limits that might be set by food supplies, and that outbreaks of rodents are caused by predator control activities, artificial or natural. The most important thing you need to know, under this paradigm, is who eats whom in your community. Since this can vary seasonally, and predators are often selective for sex and age groups, obtaining this information with quantitative rigour is not easy.

Paul Errington presented the most serious challenge to the predator paradigm more than 50 years ago by suggesting that predators consumed only the doomed surplus from rodent populations (Errington 1946). This question has been restated more recently as the question of whether predation mortality is *additive* or *compensatory* (e.g. Bartmann et al. 1992). Errington suggested that it was often compensatory. This question can be answered directly by removing predators or indirectly by showing what fraction of mortality is due to predation kills. There are considerable problems with inferring predation limitation from predator kills alone. If territoriality causes dispersal movements, or parasites cause debilitation, or food shortage causes poor condition, predators may be the executioners rather than the primary cause of population changes (Murray et al. 1997).

The usual argument against predation as a regulating factor has been that rodents have such a high rate of reproduction, that it is impossible for predators to kill enough of them (e.g. Chitty 1938, 1996; but see Korpimäki and Norrdahl 1998). It is certainly correct that sufficient numerical and functional responses must be present for predation to be a potential regulator of rodent populations (Hanski and Korpimäki 1995). From a practical viewpoint the key is to manipulate predator numbers. For example, to see if they could reduce crop damage by house mice in Australia, Kay et al. (1994) provided perches in agricultural crops for raptors. The important point is not to be convinced that predators are limiting or regulating numbers just because predators kill many rodents. It is convenient politically to show lots of dead rodents to our political masters, but scientifically dubious to infer from these piles of dead bodies that predators are helping to alleviate pest problems.

The social paradigm

The social structure of a rodent population can affect its ecology. The social paradigm states that social interactions between individuals can lead to changes in physiology and behaviour that reduce births, and increase deaths, and thereby regulate populations. In particular, territoriality may limit the average density of rodent populations. Outbreaks of rodents are postulated in this paradigm to be caused by changes in the social environment (e.g. Krebs et al. 1995). The social paradigm is the least popular of the three paradigms under which population ecologists operate. This is usually because ecologists assume that the

social environment is primarily determined by habitat which is highly correlated with food supplies. Thus, for example, food supplies determine territory size and territory size limits population density. The problem is that other factors may influence social behaviour as well, and thus the linkage of habitat to social processes can be very loose.

Practical problems of rat and mouse control had highlighted already by the 1940s that killing of rats and mice often did not result in control, especially when the pests were at high density (Chitty 1954, p. 6; Elton 1954). Achieving controls in rat populations has typically involved intensive large-scale campaigns of killing rats either directly or by poisoning (see Singleton et al., Chapter 8). Only recently has the possibility of using other methods of control like parasites (Singleton and McCallum 1990) or immunocontraception (Caughley et al. 1992; Chambers et al. 1997) been able to be explored.

The social paradigm has highlighted the role of immigration in local population dynamics. Removal experiments on rodents and other small mammals have illustrated the difficulties of controlling rodents by increasing mortality. Figure 2 illustrates one of the first experimental field removal studies on voles. In spite of very high and continuous mortality imposed by removals, the vole population continued to maintain high density and grow via immigration. Sullivan and Sullivan (1986) obtained a similar result for snowshoe hares. After a series of laboratory and field studies it became clear to ecologists that pest species with high turnover (high reproduction, high mortality, short generation times) are most

sensitive to reductions in fecundity rather than increases in mortality rates (Figure 3) (Stenseth 1981a; Lebreton and Clobert 1991).

The fence effect (Krebs et al. 1969) is one example of an experimental result that was completely unanticipated by the food or the predator paradigms (Krebs 1996). If fencing a vole population without altering the food supply or the predator fauna could produce a 3–4-fold increase in population density, what role are immigration and emigration playing in population regulation? Lidicker (1962) had raised this question long ago but few rodent workers have responded to analyse this phenomenon (Ostfeld 1994). Unfortunately if you are interested in pest control you do not wish to find a procedure that will increase rodent density! My point is that surprise results that are unexpected under the conventional wisdom can result from ignoring social processes in rodent populations.

I do not wish to argue the merits of the social paradigm here. The important point for those interested in pest control is whether or not it suggests any kinds of manipulations that could reduce pest numbers. To date the major contribution of the social paradigm to rodent pest management has been to show that dispersal and social structure can render useless simple forms of pest control via mortality (e.g. Sullivan and Sullivan 1986).

OPTIMAL POPULATION STUDIES

Given these three paradigms, what ought we to be doing in rodent population studies? We can start by asking what an ideal world of population data would look like. It would have four components.

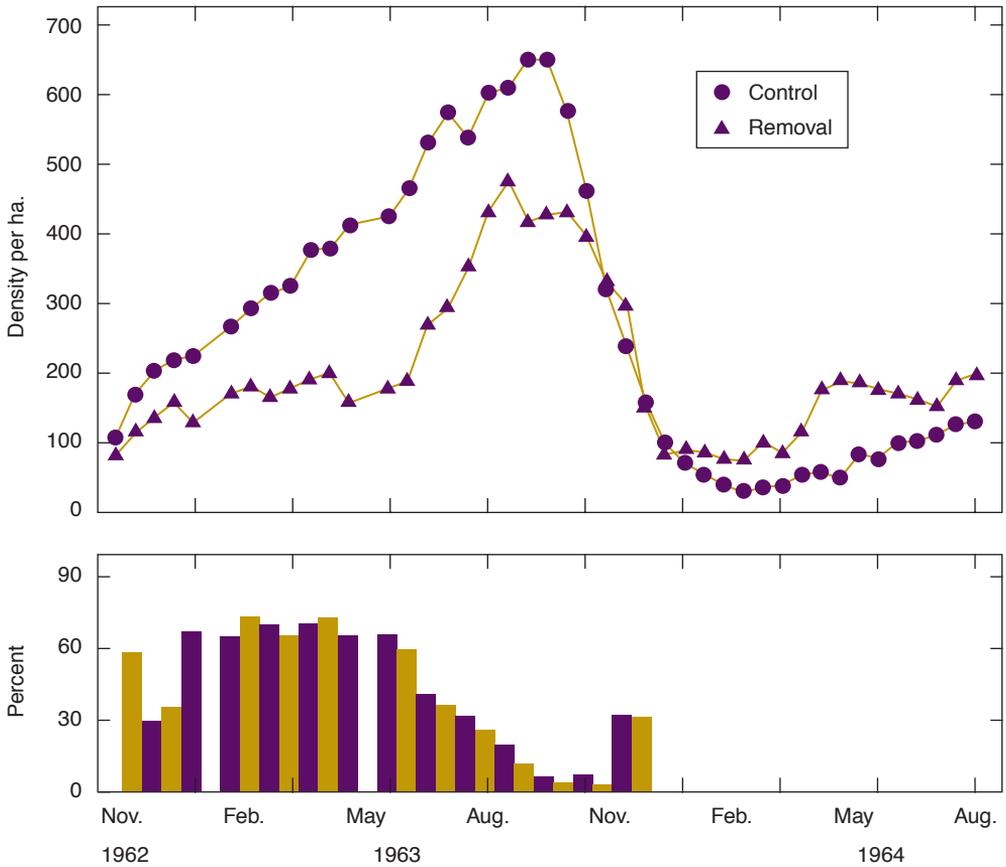
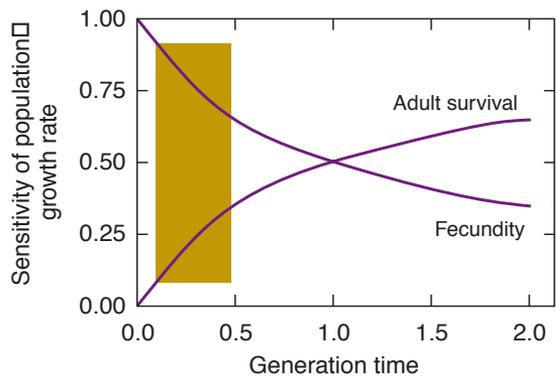


Figure 2. A removal experiment on the California vole (*Microtus californicus*). All adult voles were removed every two weeks from the removal area of 0.8 ha. From November 1962 to July 1963 an average of 62% of the population was removed every two weeks with little impact on population growth because of immigration (after Krebs 1966).

Figure 3. Relative sensitivity of the population growth rate to survival after weaning and to fecundity for mammal populations. The shaded area is the zone occupied by many rodent pests (modified after Lebreton and Clobert 1991).



Time scale

We would like to have data covering at least 10 of the population events shown by the species. If we are studying an annual cycle of rice rats in Indonesia, we would like 10 years of detailed data to show the kind of variation we might expect in the system. Ecologists like to think that they can completely sample the range of behaviours of populations in a few years. We should be more modest.

Spatial scale

We would like data from many populations spread over the geographic range of the species. The spatial resolution of these data would depend on the covariation among sites in a given neighbourhood. There are so few data of this type available for small rodents that it is a necessary part of future work. In a few cases we have these data—house mouse outbreaks in Australia (Mutze 1990), *Clethrionomys rufocanus* on Hokkaido (Stenseth et al. 1996). In particular pest control problems the spatial scale may seem to be irrelevant, but it is not if we remember that the local spatial scale can also be critical (Stenseth 1981a). The concern about dispersal and population structure has focused attention on the need to find out what a local population is and how extensively we need to manipulate populations to solve pest problems (Lidicker 1995). I think it is fair to conclude that virtually all field studies of small rodents to date have been done on too small a spatial scale.

Individual scale

We need to understand the mechanisms behind population changes, and we can

obtain this understanding only by having detailed data on individuals. This point is too rarely recognised in pest control studies. The critical data needed on individuals depends on the mechanisms proposed to explain the dynamics. If you are concerned about the role of barn owls as predators causing population changes, you must measure the difference in rodent numbers between places with and places without barn owls. If you think infanticide reduces early juvenile survival, you must obtain data on the frequency of infanticidal intrusions in different populations (Wolff and Cicirello 1989).

Community scale

Most rodent studies are single-species population studies but we should consider that it may be more fruitful to analyse interactions between species in the community as potential influences on dynamics. We typically think only of predators but should consider parasites and diseases as well (Saitoh and Takahashi 1998). In most pest rodent studies, competition for resources between species is presumed to be minimal and single-species interactions are paramount so that these community interactions can be ignored. Generalist predators are perhaps the most common factor operating on small mammals in which community interactions, including indirect effects (Menge 1997), need to be considered.

WHAT DO WE HAVE ALREADY?

Given this ideal world, we should take stock of what we have already accomplished and then move on to what we are lacking. Three strengths stand out.

- ▶ Population ecologists are fortunate in having a set of good quantitative methods for dealing with the arithmetic of population change. From the Leslie matrix to metapopulation models, there is quantitative rigour in abundance. The importance of this is not always appreciated by population ecologists, yet it is one of the great intellectual achievements of this century. We can use this arithmetic to balance the books. If we know the birth rates and death rates of a population (as well as immigration and emigration) we can compute exactly the rate of population increase or decrease. We need to use this more often to check on our estimates of these parameters (e.g. Haydon et al. 1999). For many rodent pests, control through increasing mortality is the only option available. For these cases quantitative demographic models can estimate the mortality required to reduce a population a specified amount in order to plan an optimal control program.
- ▶ Second, we have a set of good paradigms for analysing population regulation and limitation. I have outlined these above, and others can be articulated. The importance of being able to articulate clear, testable hypotheses is underappreciated in ecology (Platt 1964; Underwood 1997). Prediction, absolutely essential for scientific respectability, is almost unknown in population ecology (Peters 1991).
- ▶ Third, we have good field methods for estimating population parameters to feed into quantitative models and into statistical analysis of our experiments. Population estimation methods have been extensively improved (Pollock et al. 1990), elegant

methods for analysing survival rates are available (Lebreton et al. 1993), and statistical methods for analysing reproductive changes and separating immigration from births are being developed (Nichols and Pollock 1990; Nichols et al. 1994). We have the demographic tools to understand rodent populations with a level of precision that was not available 25 years ago.

WHAT ARE WE LACKING?

I address here six problems that I think are central to future studies on rodent populations. They are not in any particular order of importance, since some are more relevant than others to particular situations.

Good methods for spatial dynamics

One of the contributions of the social paradigm to rodent population dynamics has been the stress on the importance of immigration and emigration for understanding population changes. But we still lack good methods for studying the spatial aspects of populations. Radio-telemetry has made it possible to get some data on individual movements, but we are rarely able to do it on a scale that would be sufficient to get a broad picture of landscape dynamics. We know too little about how we should structure our studies of spatial processes. Should we have many small trapping grids or a few very large grids? How large an area should we attempt to study? What fraction of movements that we can document are genetically effective (i.e. the immigrant individual survives, breeds and leaves offspring rather than dies after immigrating)? We have much to learn about

just how to study spatial dynamics successfully in rodents, yet spatial processes underlie all of the problems of pest management. If we can reduce rats on one rice farm, will the neighbouring farms be affected or not? Much empirical work needs to be done on these questions. We can model pest populations as metapopulations in space but if we do not know the linkage parameters for these populations, our models will not be very useful.

Long-term experiments on limitation

There are no long term experiments on population limitation in any rodent species. If we feed a population for two years, we often get a population increase (Boutin 1990). What happens if we continue this experiment for 10 years? Is the system in equilibrium after two years so that we will learn nothing more from the longer study? There are numerous examples in ecology of short-term effects that were not sustained or even were reversed in the longer term (Norby et al. 1992; Wilsey 1996). There are also many examples from pest control in which initial encouraging results were followed by failures (DDT resistance, anticoagulants). The message is to be cautious about long-term conclusions.

Good interplay of models and field studies

Many ecologists have lamented the lack of interaction between field ecologists and modellers (e.g. Kareiva 1989). There are signs that this is finally breaking down (Stenseth and Saitoh 1998) but I think it is a failure on both sides that holds back progress. Models can help us to explore the

logical consequences of assumptions we make in field experiments, and provide a quantitative estimation of the anticipated effect sizes. I think it is particularly important that rodent pest control studies incorporate both adequate controls and modelling studies as part of their overall approach.

Methods for evaluating weather-driven hypotheses

Climatic change is the wave of the future and we should be more concerned that our understanding of rodent systems will be transient and modified by weather changes. Hypotheses about weather-driven events are difficult to test. Post-hoc correlational studies are useful but inconclusive. They test more the cleverness of the statistician than the reality of the biological cause. We need to state weather hypotheses clearly so they can be tested next year, not last year, and we need to abide by the simple rules of experimental falsification when our predictions fail. Ad hoc explanations are available by the shipload for ecological systems, and we should not get in the habit of using them to bail out our failures of understanding. The exact mechanisms by which weather acts on populations need to be determined, since we need to know whether births or deaths are driving the change.

Economic and environmental analyses of pest control alternatives

This is not my area of speciality but I would like to think that we should aim in pest control work to achieve the best gain for the least cost—both environmental and

economic. If we cannot achieve this, e.g. because the lowest economic cost method produces the highest environmental damage, we need to state this clearly so that the public can make an informed decision about alternatives.

Strategies for analysing the pest community of crops

In viewing rodent pests as single-species populations we overlook the broader strategy of looking at the whole community of pests of a particular crop. If the pests are truly independent, we can work on them one by one. But community interactions have ways of producing surprises via indirect effects (Holt 1987; Menge 1995), and we should be preemptive in looking for these possibilities.

CONCLUSION

The ivory tower of basic research studies on rodents has contributed little to the practical successes of rodent pest management, either short or long term. Much more insight has flowed in the opposite direction, and our understanding of rodent dynamics has been greatly improved by the practical studies of rodent pest control. What basic ecology can contribute to pest management is in the methods of study needed. The need for clear hypotheses, rigorous experimental tests based on good knowledge of natural history, a sceptical view of existing ideas, and the need to measure our successes and failures—all of these features of good science should be part and parcel of rodent management.

The major deficiencies of rodent population studies as we move into the new

millennium are three. We need to apply the insights of theoretical ecology, behavioural ecology, physiology, and genetics to rodent pest problems. A promising start in this direction is immunocontraception, (Chambers et al. 1997; Chambers et al., Chapter 10). We need studies of tropical species in varied tropical environments, since much of our knowledge of rodent ecology comes from the Temperate Zone (c.f. Leirs et al. 1996). Finally, we need more studies of parasites and diseases in field populations. Conventional wisdom suggests that they are of little impact on highly fecund rodents, but their potential for biological control is largely untested (c.f. Singleton and McCallum 1990). There are many experiments waiting to be done and much promising modelling ahead with the goal of understanding population processes in rodents and at the same time alleviating the suffering caused by rodent pests around the world.

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