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Author(s): Charles J. Krebs
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The experimental approach to rodent population dynamics*

Charles J. Krebs

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Four paradigms can be followed to help us understand the dynamics of rodent populations. *Natural observations* are the traditional way to do ecology and it is important to have a good description of the population changes that are to be explained. *Laboratory experiments* were used in the 1940s and 1950s but provided little insight into events in the field. *Field experiments* began in the 1950s and have provided the greatest insights into the factors causing changes in numbers. Six factors have been manipulated in field experiments: food, predators, cover, density, physiological condition, and genetic composition. Field experiments can be used to test single-factor or multi-factor hypotheses of population regulation. They have the additional advantage of defining operationally verbal expressions like "food-limitation" that provoke fuzzy thinking. There is no need to separate natural observations from field experiments because they are the "control" for any manipulation done in the field. *Mathematical modelling* would seem to be the best of all possible worlds, but in rodent population dynamics it has been the worst because we do not know what the relevant variables to model are. Mathematical models are not a means of discovery and cannot be used to reject logically impossible ideas in the real world. Stenseth's attempt to reject the Chitty hypothesis as logically impossible is itself logically impossible. Whether the Chitty hypothesis is correct or not can be determined only by field experiments. Nor are mathematical models useful for defining concepts operationally in ecology, and I doubt if models ever produce new principles in ecology. I argue that the only useful goal for mathematical modellers in rodent ecology is to analyze how particular variables (like female territoriality) may affect population dynamics. This goal can be achieved only by a closer liaison between modellers and field ecologists at every step in the analysis.

C. J. Krebs, Dept of Zoology, Univ. of British Columbia, Vancouver, B.C., Canada V6T 2A9.

Introduction

Rodent population ecology is a microcosm of the struggle within ecology between competing paradigms of progress. Four approaches are commonly used in an attempt to understand the dynamics of rodent populations: natural observations, laboratory experiments, field experiments, and mathematical modelling. In practice, no one argues that we can get along without all of these approaches, but there are clear advantages and disadvantages to each approach. I shall try to enumerate the strengths and weaknesses of each approach and to argue that in our present state of ignorance we should be spending most of our time doing field experiments and precious little time making mathematical models. I will illustrate these conclusions with some suggested experiments that can expedite our understanding of rodent population dynamics.

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Tab. 1. Strengths and weaknesses of different approaches to the study of rodent population dynamics. (Modified from Diamond 1986).

Component	Laboratory experiments	Field experiments	Natural observations	Mathematical modelling
1. Environmental control – Variables held constant	high	low	none	highest
2. Presence of controls (unmanipulated sites) and experimentals	yes	yes	no	no
3. Randomization of treatments	yes	yes	no	–
4. Time scale	short	moderate/long	longer	longest
5. Spatial heterogeneity present	not usually	yes	yes	possibly
6. Measurement problems	low	high	high	none
7. Range of manipulations possible	high	moderate	moderate	high
8. Realism	low to moderate	high	high	low
9. Generality	low	moderate	high	low/high

Four paradigms

Natural observations

The traditional approach to understanding rodent population changes is to observe natural populations and to try to make sense of the observations a posteriori. This approach was necessary in the past because before we can explain a phenomenon, we need a reasonably accurate description of it. This descriptive phase of the study of rodent populations occurred from about 1925 to 1955, and in a few unusual species (e.g., *Myopus schisticolor*) and unknown faunas (South America) is still going on today.

Natural observations on rodent populations can also be used to test hypotheses, and this is in fact another use of the experimental method. The essential feature of an *experiment* in science is a set of observations designed to test a hypothesis (Medawar 1957). Not all experiments are manipulative, a point commonly misunderstood, and non-manipulative or "natural experiments" can be a valuable way to proceed in ecological studies (Diamond 1986). For example, all hypotheses about *weather* in rodent population dynamics must be tested by natural observations because we cannot yet manipulate weather in natural ecosystems. The major disadvantage of natural experiments is that they may be inefficient if the conditions to be analyzed occur only rarely. More effort could be taken to search out contrasting types of populations to utilize natural experiments.

Natural observations are a necessary part of all field experiments because they are the "control" against which all the changes in the "experimental" populations are studied. For this reason there is at the present time no need to set up a rodent study that makes only natural observations without a hypothesis to test. You would be better advised to set up a field experiment in which the natural observations will be included as the "control". The fundamental weakness of natural observations is the absence of the contrast between experimental and control sites.

Laboratory experiments

In an ideal world laboratory experiments on rodent populations would quickly test the variables hypothesized to be relevant to understanding dynamic changes in births and deaths. This was the belief of the 1950s when a large number of confined populations (particularly of *Mus musculus*) were studied. These studies, remarkable in their design, rich in their control of environmental conditions, and accurate in their vital statistics, have provided little or no understanding of real-world populations. Redhead (1986), for example, points out how little is known about the factors that generate *Mus musculus* outbreaks in the wheatlands of southeastern Australia. Laboratory experiments were useful in suggesting that spacing behaviour might be relevant to understanding population changes (Clarke 1955, Crowcroft 1966, Christian 1971). The reason for the failure of laboratory studies to increase our understanding of population dynamics is a complete contrast to all other areas of biology in which laboratory studies are essential to all progress. Why should this be? Laboratory populations simultaneously have too many variables altered – food quantity, food quality, predation rates, disease transmission, parasite transmission, amount of space, seasonality – so that when we observe, for example, that laboratory populations of *Microtus* do not fluctuate cyclically, we do not know which variables to blame for this change in population dynamics.

Consequently, almost no one does laboratory population studies any more in spite of their strong points (Tab. 1) The lack of spatial heterogeneity in laboratory studies is possibly the critical shortcoming with respect to studies of rodent population dynamics. In principle this shortcoming can be overcome with sufficient knowledge, cleverness, and facilities (Crowcroft 1966) but these are rarely achieved. It may be that laboratory studies will provide essential detailed analyses of some of the features of rodent population dynamics discovered in field populations. One example is the analysis of reproductive suppression in *Clethrionomys* females, reported by Bujalska (1970) from field observations and

Tab. 2. Some principles of rodent population dynamics that have been established by field experiments. This is not an exhaustive reference list but only illustrative.

Principle	Manipulation	References
1. Carrying capacity is partly determined by food supply	add food	Cole and Batzli 1978, Taitt 1981, Taitt and Krebs 1981
2. Cyclic population declines cannot be a direct consequence of food shortage	add food through a decline	Krebs and DeLong 1965, Henttonen 1986, Cole and Batzli 1978, Desy and Thompson 1983
3. Winter mortality is increased by predation	exclude predators	Taitt and Krebs 1983
4. Dispersal is necessary for population regulation in voles	fencing experiment	Tamarin et al. 1984, Beacham 1980, Gaines et al. 1979
5. Spacing behaviour of female voles limits recruitment	sex-specific removals	Boonstra 1978, Boonstra and Rodd 1983
6. Large numbers of surplus voles occur in natural populations	total removal experiments	Krebs 1966, Baird and Birney 1982

analyzed in enclosures by Saitoh (1981) and Bondrup-Nielsen and Ims (1986).

Field experiments

Field experiments are inherently attractive and impossibly messy. They are attractive because they include a "control" which becomes the yardstick by which the experimental treatment can be judged. The use of a "control" is an absolutely essential feature of all sciences that deal with complex systems in which scientific explanation consists of explaining the *differences* between the "control" and the "experimental" populations. Field experiments are messy because it is difficult to match sites so that all relevant conditions are equal at the start of the manipulation, and replication is rarely as frequent as anyone would like. Nevertheless, field experiments are the closest we can come in ecology to matching the ideal procedure of laboratory biology (Tab. 1).

Field experiments in rodent population ecology have concentrated on manipulating six factors: (1) food supply; (2) predators; (3) cover; (4) density (including sex ratios); (5) physiological condition of individuals, and (6) genetic composition of population. Tab. 2 summarizes some results from these types of manipulations.

Food supply manipulations

Most feeding experiments have been done by adding food (e.g., Cole and Batzli 1979, Taitt 1981), and I know of only one food-reduction experiment on rodents (S.-A. Bengtson et al. 1986 ms). In a few cases food supplies have been manipulated indirectly by fertilizing the plants (Krebs and DeLong 1965, Batzli 1983, Henttonen 1986). These experiments have supported two generalizations for small rodents; (1) that carrying capacity can be increased by increasing the food supply and reduced by reducing it; and (2) that population changes (particularly cyclic declines) cannot be prevented by food manipulations.

The power of field experiments to answer questions about rodent population dynamics has been shown most clearly by contrast with the many inconclusive attempts to evaluate the food hypothesis since Lack (1954) enunciated it. For 20 years the food hypothesis was the guiding light of the Berkeley group led by Frank Pitelka, and their operating philosophy was to test this hypothesis by natural observations rather than by field experiments. The food hypothesis has now been rejected as an explanation of the lemming cycle (Batzli et al. 1980). It should not take us 25 years to reject a false hypothesis in population dynamics. If we adopt an experimental approach, the time should be no more than 5–6 years.

Predator manipulations

There have been relatively few attempts to manipulate predators of small rodents to test hypotheses about the role of predation in population dynamics. Predators have been removed on a large scale by gamekeepers in Britain and Europe and by hunters and trappers in North America. But in only a few cases have precise manipulations been done with a suitable control population. The most elegant experiment now being done is at Lund, where Sam Erlinge is excluding predators from 1-ha plot and comparing the effect of their absence on the local vole populations. We need much more detailed experimental work on predation to test recent hypotheses about cyclic density changes (Henttonen 1986).

Cover manipulations

Cover is one variable that can be manipulated relatively easily on small areas (Taitt and Krebs 1983). Few people have done so, perhaps because cover may affect two variables at once. Since many vole predators hunt by sight, cover will usually make their prey less available. At the same time cover increases the spatial complexity of a habitat and thus may reduce social interactions. These two effects of cover may be disentangled by excluding predators with some form of netting without changing the cover. Birney et al. (1976) have shown how important cover is to the existence of cycles in *Microtus* populations. It is surprising that cover is so rarely studied by small mammal ecologists.

Density manipulations

One of the easiest variables to manipulate is population density, and many experiments have been done in this way (reviewed in Boonstra and Rodd 1983, Krebs 1985). The most creative removal experiments have involved sex-ratio manipulations and these manipulations are a good example of how field experiments can produce demographic situations that would never be observed in a natural population no matter how long the study. There is still much scope for these kinds of manipulations, particularly for experiments that remove or reduce certain genotypes or phenotypes within the population. Density manipulations in open populations are complicated by rapid immigration that may be hard to prevent.

Physiological manipulations

The more precise experiments of altering the physiological state of individual voles were pioneered by Gipps and Jewell (1979) and Gipps et al. (1981). Relatively few attempts have been made to do these experiments, yet they represent a necessary increase in the level of precision for the testing of intrinsic hypotheses of population regulation (Krebs 1985).

Genetic composition

I know of only one experiment that has tried to measure the impact of artificial selection on a vole population (LeDuc and Krebs 1975). The utility of this type of manipulation is limited by our ability to identify interesting genotypes in field populations. The most obvious experiment waiting to be done along these lines is to manipulate the frequency of the sex-ratio genotypes of the wood lemming *Myopus schisticolor* and the varying lemming *Dicrostonyx* (Fredga 1983).

Taken together, all this argues that field experiments are the most efficient way to test specific hypotheses about the factors driving rodent population dynamics. This is true whether or not one supports the multifactor model of regulation (Hilborn and Stearns 1982, Lidicker 1985) or whether one is addicted to single factor explanations. Multifactor models must be testable. They demand an increased level of sophisticated experimental design that has been used for a long time in agriculture and psychology. Because a model is complex is not a sufficient reason for avoiding field experiments.

One additional advantage of field experiments is that they provide a mechanism for defining concepts operationally. For example, many ecologists argue about "food-limitation" of populations. Food may be said to limit population density whenever the addition of food is followed by an increase in density. The experimental manipulation defines the concept unambiguously. Other examples can be easily cited. Do "surplus" individuals exist in a population? Do a removal experiment and see if replacement occurs. Does predation cause the lemming crash? Remove predators and see if the crash occurs. The use of field experimentation as a mechanism of operational definition in ecology is one important way of reducing futile controversy about population and community dynamics.

Mathematical modelling

Mathematical modelling would seem to have the best of all possible worlds (Tab. 1). It is not bothered by the messy nature of ecological field measurements with all their associated errors. It controls all variables absolutely, and provides an infinite range of possible manipulations of variables, and it does all of this with electronic speed so that 100 years of lemming cycles can be generated in 3 or 4 seconds of computing time. Why are we all not mathematical modellers then?

Mathematical modelling is a type of formal logic that derives the logical consequences of certain assumptions about population processes. In a science that knows all the elements, all the relevant variables, formal logic is of great value in searching out testable consequences. But the problem is that you must know what the relevant variables are before you can set up a mathematical model. In particular for small rodent populations you must decide whether to build a model based on food supply (Stenseth et al. 1977), predation (Erlinge et al. 1984), spacing behaviour (Krebs 1985), population genetics (Hunt 1982), lunar periodicities (Archibald 1977) or some combination of these variables. Which of these variables are relevant to understanding rodent population dynamics is the central problem and focus of much controversy in mammalian ecology today.

If you know which variables are indeed relevant to your rodent system, building a model becomes a most significant and important exercise. As Stenseth (1985a) has clearly pointed out, a formal model is the only way an ecologist can follow through all the assumptions of verbal models in a quantitative and rigorous way. The argument is not "*are* mathematical models useful?" but rather "*when* are mathematical models useful?". In particular, in rodent population ecology today, do we know enough to construct useful models? I answer *no* to this question because we have done too few experiments to isolate the relevant factors driving population dynamics.

An excellent example of both the utility and the futility of modelling is the Chitty Hypothesis (Stenseth 1981, 1985b). Chitty proposed that a necessary factor for generating population cycles in small rodents is a change in spacing behaviour coupled with changes in the genetic composition of the population (Chitty 1967). Stenseth (1981) tried to model the Chitty Hypothesis by assuming that the proposed intrinsic changes were *sufficient* to generate cycles, and he rejected this possibility. However, when extrinsic variables were added to the Chitty model, Stenseth (1981) found that cycles could be obtained. Later he seems to recant this: "Chitty's hypothesis is unable to explain the occurrence of regular cycles" (Stenseth 1985b).

How are we to interpret this rejection of the Chitty hypothesis? At least three different models have been published which demonstrate that the general mechanisms proposed by Chitty can lead to population cycles. Anderson (1975) produced a simple simulation model based on quantitative genetics that resulted in population cycles. Hunt (1982) produced a mathematical model of the Chitty hypothesis, using a one-locus, two allele system with density-dependent selection. Page and Bergerud (1984) produced another simulation model of the Chitty hypothesis and applied it to 10-year grouse cycles. Some, or all, of these three models may be rejected, as Stenseth (1985b) claims, if their biological predictions are incorrect. But we need to make further observations to find out if the predictions are correct and we cannot decide these empirical issues without further evidence. For example, Anderson's (1975) model will produce cycles only if the heritability of spacing behaviours is above 80%. A priori, this is a very high value but not unheard of in rodents (Singleton and Hay 1982). To find out if this assumption is false, we have to determine what behavioural traits are important in spacing and then measure their heritability. No one has done this yet for any cyclic microtine, so we do not know whether to accept Anderson's model as valid and useful, or to reject it as biological unrealistic, as Stenseth (1985a) does.

Stenseth (1985b) argues that one advantage of mathematical models is that they can allow us to reject logically impossible ideas. He gives the Chitty hypothesis as an example of a theory that is logically implausible. I do not see how this conclusion can be sustained, given the three models of the Chitty hypothesis discussed above. Moreover, I doubt that there is a single current idea in rodent population dynamics that could be excluded as logically impossible. Many hypotheses are likely to be incorrect but all are logically possible.

A second advantage of mathematical models, according to Stenseth (1985b), is that we are forced to define concepts operationally. An example is habitat heterogeneity. Stenseth (1985b) produced a model incorporating habitat heterogeneity for *Clethrionomys* populations; the model used one optimal and one suboptimal patch, and Stenseth found that the degree of density fluctuation was decreased by incorporating habitat heterogeneity in the model. We are left to conclude that this may be a general result. But the fact is that any field ecologist will see habitat heterogeneity as a complex idea, incorporating seasonal shifts in habitat requirements, conflicting habitat demands with respect to feeding, breeding, and avoiding predators, and random settlement effects. None of these are easy to study or understand in terms of population dynamics, and we field ecologists are given no insight into how to measure and interpret habitat heterogeneity on the basis of the modelling so far done. Modelling operationally defines such a concept by trivializing it.

A third advantage to mathematical modelling, according to Stenseth (1985b), is that new principles may emerge from mathematical analysis. An example he cites is Gause's competitive exclusion principle. I agree with Stenseth's interpretation here, but I would add only that this new principle from Lotka and Volterra, graphed to Gause's laboratory experiments, has led more ecologists into futile works and blind alleys than any other ecological idea in this century (Lewin 1983). It is not something I would be proud of were I a modeller.

A fourth advantage of mathematical modelling, according to Stenseth (1985b), is that a model may suggest how the same ecological factor (e.g., territoriality) can produce population stability under some conditions and population fluctuations under different conditions. I think this is the one useful thing that mathematical modelling can do for field ecologists, and I hope this is the goal that this issue achieves. The modeller working to achieve these goals must maintain close liaison with the field ecologist. Stenseth (1985b) discusses some models for *Clethrionomys* populations that attempt to reach these goals. From the viewpoint of a field ecologist, the models developed so far do not bridge the gap to the types of data measured in the field. As the two groups move closer together, we may expect to see a measure of more rapid progress in the field experiments that must in the end test all hypotheses about rodent population dynamics.

Mathematical modelling is one of the sacred cows of modern ecology, and few seem to recognize the tremendous distortion it has had on the development of ecological theory. Most modelling is directed to explaining things a posteriori. Given the simplification that must occur in modelling and the complexity of all ecological events, anyone can explain anything a posteriori given enough time and trouble. This does not advance ecological knowledge, which will improve more rapidly as we try to test predictions with field experiments.

Conclusion

I have argued in this paper that we have passed the natural observation phase of rodent population work and should concentrate our efforts on field experiments.

We are moving toward a time when mathematical modelling will be a useful paradigm, but I do not think we are yet in this phase of development. We do not yet know the elements of the rodent population puzzle well enough to model it usefully.

When mathematical modelling is undertaken, I would plea for more interaction and understanding between modellers and field ecologists. Because a field worker cannot write differential equations does not mean that he or she has no useful ideas about natural population regulation. Modellers should strive to lay out their assumptions in a clear form so that field ecologists can test them with real data. For example, Stenseth (1985b: Fig. 2) assumes that the adult mortality rate is a positive linear function of population density in *Clethrionomys*. Surely there are some field data available to test this assumption, and it would be a useful closing of the loop now for *Clethrionomys* field workers to take Stenseth's graphs and put some real data points on them. In this way we can make models for rodent populations that are realistic and general so we have the best of all paradigms.

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References

Anderson, J. L. 1975. Phenotypic correlates among relatives, and variability in reproductive performance in populations of the vole, *Microtus townsendii*. – Ph. D. Thesis, Univ. of British Columbia, Vancouver.

Archibald, H. L. 1977. Is the 10-year wildlife cycle induced by a lunar cycle? – Wildl. Soc. Bull. 5: 126–129.

Baird, D. D. and Birney, E. C. 1982. Pattern of colonization in *Microtus pennsylvanicus*. – J. Mammal. 63: 290–293.

Batzli, G. O. 1983. Responses of Arctic rodent populations to nutritional factors. – Oikos 40: 396–406.

– , White, R. G., MacLean, S. F., Pitelka, F. A. and Collier, B. D. 1980. The herbivore-based trophic system. – In: Brown, J., Miller, P. C., Tiezen, L. L. and Bunnell, F. L. (eds), An Arctic Ecosystem. Dowden, Hutchinson, and Ross, Stroudsburg, PA, pp. 335–410.

Beacham, T. D. 1980. Dispersal during population fluctuations of the vole, *Microtus townsendii*. – J. Anim. Ecol. 49: 867–877.

Birney, E. C., Grant, W. E. and Baird, D. D. 1976. Importance of vegetative cover to cycles of *Microtus* populations. – Ecology 57: 1043–1051.

Bondrup-Nielsen, S. and Ims, R. A. 1986. Comparison of maturation of female *Clethrionomys glareolus* from cyclic and noncyclic populations. – Can. J. Zool. 64: 2099–2102.

Boonstra, R. 1978. Effect of adult Townsend voles (*Microtus townsendii*) on survival of young. – Ecology 59: 242–248.

– and Rodd, F. H. 1983. Regulation of breeding density in *Microtus pennsylvanicus*. – J. Anim. Ecol. 52: 757–780.

Bujalska, G. 1970. Reproductive stabilizing elements in an island population of *Clethrionomys glareolus* (Schreiber 1780). – Acta Theriol. 15: 381–412.

Chitty, D. 1967. The natural selection of self-regulatory behaviour in animal populations. – Proc. Ecol. Soc. Aust. 2: 51–78.

Christian, J. J. 1971. Population density and reproductive efficiency. – Biol. Reproduction 4: 248–294.

Clarke, J. R. 1955. Influence of numbers on reproduction and survival in two experimental vole populations. – Proc. R. Soc. London Ser. B, 144: 68–85.

Cole, F. R. and Batzli, G. O. 1979. The influence of supplemental feeding on a vole population. – J. Mammal. 59: 809–819.

Crowcroft, P. 1966. Mice all over. – G. T. Foulis, London.

Desy, E. A. and Thompson, C. F. 1983. Effects of supplemental food on a *Microtus pennsylvanicus* population in central Illinois. – J. Anim. Ecol. 52: 127–140.

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. – In: Diamond, J. and Case, T. J. (eds), Community ecology. Harper and Row, New York, pp. 3–22.

Erlinge, S., Göransson, G., Högstedt, G., Jansson, G., Liberg, O., Loman, J., Nilsson, I. N., von Schantz, T. and Sylvén, M. 1984. Can vertebrate predators regulate their prey? – Am. Nat. 123: 125–133.

Fredga, K. 1983. Aberrant sex chromosome mechanisms in mammals. – Differentiation 23: S23–S30.

Gaines, M. S., Vivas, A. M. and Baker, C. L. 1979. An experimental analysis of dispersal in fluctuating vole populations: demographic parameters. – Ecology 60: 814–828.

Gipps, J. H. W. and Jewell, P. A. 1979. Maintaining populations of bank voles, *Clethrionomys glareolus*, in large outdoor enclosures, and measuring the response of population variables to the castration of males. – J. Anim. Ecol. 48: 535–555.

– , Taitt, M. J., Krebs, C. J. and Dundjerski, Z. 1981. Male aggression and the population dynamics of the vole, *Microtus townsendii*. – Can. J. Zool. 59: 147–157.

Henttonen, H. 1986. Causes and geographic patterns of microtine cycles. – Ph. D. Thesis, Univ. of Helsinki, Finland.

Hilborn, R. and Stearns, S. C. 1982. On inference in ecology and evolutionary biology: the problem of multiple causes. – Acta Biotheor. 31: 145–164.

Hunt, F. 1982. Regulation of population cycles by genetic feedback: existence of periodic solutions of a mathematical model. – J. Math. Biol. 13: 271–282.

Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. – Ecol. Monogr. 36: 239–273.

– 1985. Do changes in spacing behaviour drive population cycles in small mammals? – In: Sibly, R. M. and Smith, R. H. (eds), Behavioural ecology. Blackwell, Oxford, pp. 295–312.

– and Delong, K. T. 1965. A *Microtus* population with supplemental food. – J. Mammal. 46: 566–573.

Lack, D. 1954. The natural regulation of animal numbers. – Clarendon Press, Oxford.

LeDuc, J. and Krebs, C. J. 1975. Demographic consequences of artificial selection at the LAP locus in voles (*Microtus townsendii*). – Can. J. Zool. 53: 1825–1840.

Lewin, R. 1983. Santa Rosalia was a goat. – Science 221: 636–639.

Lidicker, W. Z. Jr. 1985. Dispersal. – In: Tamarin, R. H. (ed.), Biology of New World *Microtus*. Spec. Publ. Am. Soc. Mammalogists 8: 420–454.

Medawar, P. B. 1957. A note on 'The Scientific Method'. – Pp. 71–78 in The Uniqueness of the Individual, Methuen, London.

Page, R. E. and Bergerud, A. T. 1984. A genetic explanation for ten-year cycles of grouse. – Oecologia (Berl.) 64: 54–60.

Redhead, T. 1986. Mouse-plague research for rural Australia. – CSIRO, Rodent Control Research Laboratory, Canberra.

Saitoh, T. 1981. Control of female maturation in high density populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. – J. Anim. Ecol. 50: 79–87.

Singleton, G. R. and Hay, D. A. 1982. A genetic study of male social aggression in wild and laboratory mice. – Behavior Genetics 12: 435–448.

Stenseth, N. C. 1981. On Chitty's theory for fluctuating populations: the importance of genetic polymorphism in the generation of regular density cycles. – J. Theor. Biol. 90: 9–36.

– 1985a. Mathematical models of microtine cycles: models and the real world. – Acta Zool. Fennica 173: 7–12.

– 1985b. Models of bank vole and wood mouse populations. – In: Flowerdew, J. R., Gurnell, J. and Gipps, J. H. W. (eds), The ecology of woodland rodents. Clarendon Press, Oxford, pp. 339–376.

– , Hansson, L. and Myllymäki, A. 1977. Food selection of the field vole *Microtus agrestis*. – Oikos 29: 511–524.

Taitt, M. J. 1981. The effect of extra food on small rodent populations: 1. Deermice (*Peromyscus maniculatus*). – J. Anim Ecol. 50: 111–124.

– and Krebs, C. J. 1981. The effect of supplementary food on small rodent populations. 2. Voles (*Microtus townsendii*). – J. Anim. Ecol. 50: 125–137.

– and Krebs, C. J. 1983. Predation, cover, and food manipulations during a spring decline of *Microtus townsendii*. – J. Anim. Ecol. 52: 837–848.

Tamarin, R. H., Reich, L. M. and Moyer, C. A. 1984. Meadow vole cycles within fences. – Can. J. Zool. 62: 1796–1804.