CHAPTER
13

Are lemmings large *Microtus* or small reindeer? A review of lemming cycles after 25 years and recommendations for future work

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CONTENTS

The Biology of Lemmings
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Abstract

The demography of lemmings (*Lemmus* and *Dicrostonyx*) is similar to that of other cyclic voles. I attempt here to generalize about the demography of lemming cycles. There are few detailed studies and these are mostly confined to the summer months. Winter breeding is one of the most significant features of lemming ecology. We do not understand why lemmings breed in some winters and not in others. Juvenile losses are high in peak and declining populations, but the causes of these losses are not known. Dispersal has not been studied except anecdotally. There is a great need for detailed mark–recapture studies on lemmings.

I present four hypotheses about lemming cycles that require testing. The fence effect needs to be tested for lemmings. Heritability of spacing behaviour is predicted to be high in cyclic lemmings. Female spacing behaviour may limit recruitment at all phases of the cycle. Interspecific synchrony is postulated to arise from predation pressure in the decline phase.

Almost any detailed demographic work on lemmings would be useful but past efforts have suffered by not asking crisp experimental questions of field populations. I suggest that lemmings are large *Microtus* whose population changes are driven by changes in social behaviour, and not small reindeer whose population changes are driven by changes in food supplies, predation and disease.

INTRODUCTION

Lemming cycles are known anecdotally to almost all people, and for this reason we should try to understand both the proximate forces driving these cycles and the ultimate reasons why they occur at all. These are not easy goals to achieve. Lemmings are perhaps the most difficult small rodents to study because of their northern distribution and the difficulties of doing winter population work. It is thus understandable that Stenseth (1985) found only four references to *Lemmus* population dynamics in his search of BIOSIS from 1969 to 1983, out of a total of 4681 references on population dynamics. There is perhaps 20 times as much work done on *Microtus* populations as on lemming populations. The week-long conference on lemmings at Konnevesi brought together all the work done on lemmings; a similar conference on *Microtus* would last for months.

In this chapter I draw together the *demographic* facts about lemming cycles and use these as a springboard to suggest the most critical gaps in our understanding. All the statements I make could be wrong and if they can be corrected by further research, we will have made some progress. I restrict my discussion to the genera *Lemmus* and *Dicrostonyx* in Eurasia and North America, and do not repeat things already reviewed in Krebs & Myers (1974).

DEMOGRAPHY AND POPULATION DYNAMICS OF LEMMINGS

I consider first the general features of lemming population changes.

There are no stable lemming populations

All the populations studied are either cyclic with a 3–4 year period (Fig. 1), or are rare at such a low density that they are hard to detect (Boonstra & Krebs, unpublished data, Pearce Point, N.W.T., Canada). Lemmings thus contrast with *Microtus* and *Clethrionomys* that may show annual cycles at moderate densities both in North America and in southern Scandinavia (Taitt & Krebs, 1985; Hansson & Henttonen, 1985). It will be difficult to determine why low density lemming populations remain low; any number of environmental factors (food, predators, disease) could be involved and there will not be a general explanation for all low density populations. There could be stable, high density lemming populations that have yet to be studied.

Pitelka (1973) provided long-term snap-trap data for *Lemmus sibiricus* [*L. trimucronatus* of Chapter 3, this volume] near Barrow, Alaska. Cycles with periods

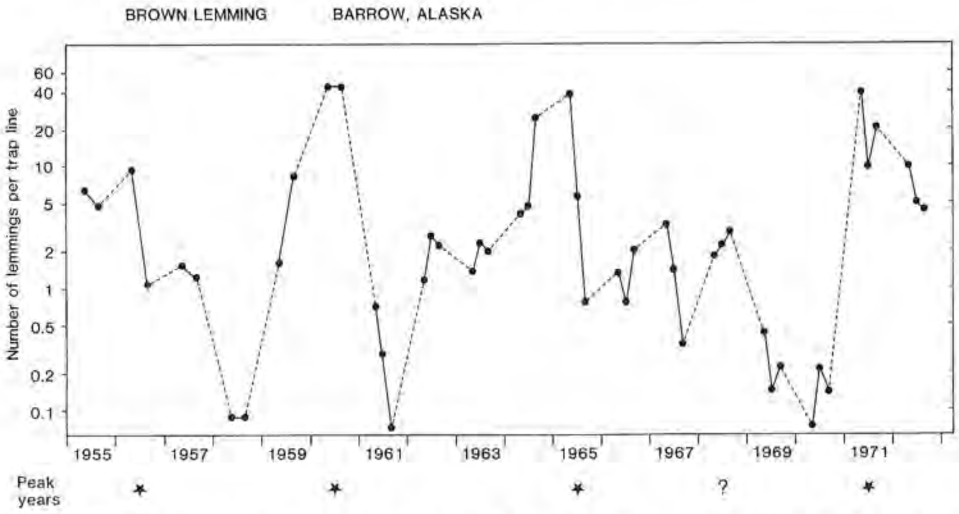

Figure 1 Brown lemming numbers (log scale) at Barrow, Alaska, 1955–1972. Data from Pitelka (1973), table 1. There is some question whether or not there was a peak in 1968. Two or three trappings were done each year in June, July, and August (see also Chapter 11, Fig. 2, this volume).

of 3–5 years occurred in these populations from 1946 to 1972, with the exception of one truncated cyclic peak in 1968 (Fig. 1).

In northern Finland lemming peaks coincide with the cyclic highs of other voles, but lemmings are not numerous in every peak (Henttonen *et al.*, 1984). At Finse in southern Norway Framstad, Stenseth & Østbye (Chapters 5 and 6, this volume) showed from 16 years of trapping data that *Lemmus lemmus* populations fluctuated with a 4-year periodicity but a highly variable amplitude. On one area of very low vegetative productivity *Lemmus* numbers also fluctuated, presumably under the influence of immigration from more productive habitats. Lemming populations that do not fluctuate because of low productivity may exist in theory (Oksanen *et al.*, 1981) but no one has yet found one in the real world.

The amplitude of lemming cycles is in the range of 25:1 to 200:1

There are almost no reliable estimates of absolute density for any lemming population. Even if we accept most of the published guesses for the density of peak populations, the density of the low phase is critical in all amplitude estimates and there are almost no data for the low phase. If we accept snap-trap indices as approximations of true densities, we can estimate the June amplitude of the *Lemmus sibiricus* population cycle at Barrow, Alaska from Pitelka's (1973) data as follows: 113-fold, 64-fold, 29-fold and 47-fold. Krebs (1964) estimated the amplitude of one *Lemmus sibiricus* cycle to be 50-fold and a *Dicrostonyx groenlandicus* cycle to be 25-fold. A simple life-table model of a lemming population suggests that only rarely could these animals increase more than 200-fold in 2 years, so these estimates of amplitude do not seem unreasonable. Pitelka (1973: 205) and Batzli *et al.* (1980: 338) suggest amplitudes of 500:1 and 1000:1 for *Lemmus* at Barrow. I think these are impossibly high.

The cyclicity index (*s*) of Stenseth & Framstad (1980) and Henttonen, McGuire & Hansson (1985) (see also Appendix-chapter 1, this volume) is 0.79 for Pitelka's (1973) *Lemmus* estimates (1955–1972) and is 0.85 for Krebs (1964) *Lemmus* data (1959–1962), when the spring (June) data are used. These indices for the autumn (August) data are 0.83 for Pitelka's population and 0.78 for Krebs' *Lemmus*. Framstad, Stenseth & Østbye (Chapter 5, this volume) reported cyclicity indices (s) of 0.98–1.08 for three populations of *Lemmus lemmus* in southern Norway, somewhat above the range observed in North American lemming populations. These values are at the maximal levels reported by Henttonen *et al.* (1985) for cyclic *Clethrionomys* populations.

Brown lemming populations in northern Alaska fluctuate less in areas where their favoured food plant *Dupontia* is rare (Batzli & Jung, 1980), as predicted by Stenseth (1978, 1986) from a general model. But it is a moot question whether all variations in cyclic amplitude can be explained nutritionally or not. In Fennoscandia most variations in the amplitude of population fluctuations of birds and medium-sized mammals are currently explained by predation pressures (Angelstam, Lindstrom & Widen, 1984).

The increase phase is the least variable phase, very rapid, and is accomplished in 1 year with overwinter population growth being most critical. The decline phase is highly variable and can occur in any season at a slow or rapid pace

There are two quite different conceptions of the lemming cycle. Some, like Stenseth (1978) and Stenseth & Ugland (1985), believe that the increase phase is slow and variable while the decline phase is sudden and less variable. Others, like Krebs & Myers (1974), contend the opposite, that the increase phase is explosive and the decline phase is most variable. The data in Krebs (1964) clearly support the second alternative. The data in Pitelka (1973) are not, I think, precise enough to answer this question definitely. The Barrow *Lemmus* data appear to me to support the second alternative rather than the first. Certainly the decline phase was highly variable at Barrow, starting in mid-winter, late winter, spring or summer. Information on the decline phase could help us to determine possible causes for the decline.

Henttonen & Järvinen (1981) reported a crash of *Lemmus lemmus* at Kilpisjarvi that occurred in late winter, March 1979. Lemming density the preceding year had not been very high, yet the decline proceeded rapidly and lemmings were very scarce already by May 1979. Framstad, Stenseth & Østbye (Chapters 5 and 6, this volume) recorded a very similar crash in late winter 1977/1978 for *Lemmus lemmus* at Finse, Norway. Pitelka (1973) described a similar late winter crash in 1968/1969 in *Lemmus sibiricus* at Barrow, Alaska. An estimate of the frequency of these 'aborted peaks' in lemmings is difficult to make. The only data are one of five cases in the Barrow, Alaska data (Pitelka, 1973) and one of four cases in the Finse data (Chapters 5 and 6, this volume). From the limited data we have, spectacular collapses seem to occur more commonly in Scandinavian populations of *Lemmus lemmus* than in North American populations of *Lemmus sibiricus* or *Dicrostonyx* spp. There is clearly an enormous shortage of quantitative data here.

The low phase of the lemming cycle is particularly lacking in data. For the Barrow *L. sibiricus* population, Pitelka (1973) showed three of four complete cycles with an extended low phase lasting 1–2 years. The Finse *Lemmus lemmus* data are even more extreme, showing a low phase from 1 to 3 years duration between cyclic peaks (Chapters 5 and 6, this volume). These lemming 'lows' seem to be longer and more severe (i.e. lower density) than the low phases described for temperate zone *Microtus* populations (Krebs & Myers, 1974).

REPRODUCTION IN LEMMINGS

Reproductive parameters provide one part of the demographic equation and lemmings are particularly interesting in their reproductive patterns.

Winter breeding is always associated with cyclic increases and a lack of winter breeding with the decline phase

The single most spectacular biological accomplishment of lemmings is their ability to breed in the winter under snow (see Chapter 4, p. 67, this volume). This physiological miracle has been little studied and I do not know why. Given the extreme environments in which lemmings live, it is tempting to argue that without winter breeding they could not cycle (Kaikusalo & Tast, 1984). One hypothesis to explain low density, non-cyclic lemming populations (if indeed they exist) could be that they are unable to winter breed. Why? In particular why, if they can breed one winter, can they not breed any winter? Presumably lemmings decide in an evolutionary sense to breed in winters when it is optimal to do so (Stenseth, 1978). What cues are they using to decide this and are all individuals capable of winter breeding?

Hansson (1984b) reviewed winter reproduction among Scandinavian small mammals, and pointed out how important it is to population changes in *Lemmus lemmus*. He suggested the need for controlled breeding experiments in laboratory conditions of lemmings collected from different cyclic phases. Here is indeed a critical experiment waiting to be done! Kaikusalo & Tast (1984) carried out this experiment with *Lemmus lemmus* but only on animals from the increase phase of the cycle.

Lemmings are not the only microtine rodents to breed during the winter and the pattern of periodic winter breeding associated with population increase is a common occurrence in *Microtus* spp. (Krebs & Myers, 1974; Hansson, 1984b; Keller, 1985). There is as yet no comprehensive explanation for winter breeding in temperate zone voles, although hypotheses abound without critical data (Keller, 1985).

Summer breeding may be curtailed at high densities

Female lemmings ought to be constantly striving to maximize their fitness, as do all animals. Thus, if we observe the cessation of reproduction in the middle of the summer growing season (Krebs, 1964), we should suspect that the costs of reproduction for lemming females have exceeded the benefits. There is no suggestion in Pitelka (1973) or in Batzli *et al.* (1980) that the Barrow population of *Lemmus* stops breeding early in the year of peak density. However, they do report that younger lemmings breed much less in high density populations, as was found by Krebs (1964).

Schaffer & Tamarin (1973) were the first to analyse these changes in reproductive effort over a population cycle. They concluded that individuals appeared to change their reproductive rate in such a way as to maximize their fitness. Ugland & Stenseth (1985) analysed this problem in much more detail. They show that the evolutionarily optimal reproductive rate will fall with population density, and that, as observed in lemmings, it is optimal to allocate resources to competitive ability rather than to reproduction under crowded conditions. It is encouraging how the field data and the theory agree in this analysis of reproductive rates (Stenseth, 1978).

The presumption is that this curtailment of breeding in the summer of the lemming peak is due to social behaviour or a shortage of 'space', and is not the result of food deficiencies (e.g. Jannett, 1984). It would be useful to test this hypothesis by feeding and removal experiments (e.g. Gilbert *et al.*, 1986) on a high-density lemming population.

Infanticide occurs in laboratory populations of the collared lemming *Dicrostonyx groenlandicus* if a strange male is introduced 1 day post partum (Mallory & Brooks, 1978). Strange males killed 37–50% of the young in 32 trials, and this infanticide could be significant in the field if it occurs in peak and declining populations.

Lemming males and females may thus have different and conflicting reproductive strategies (Mallory & Brooks, 1980).

No one has recorded infanticide in field populations of lemmings, and what little data we have on peripheral topics is rather negative. Heske, Ims & Steen (Chapter 23, this volume) removed female *Lemmus lemmus* from one area during a decline summer and could detect no immediate impact on recruitment or survival of juveniles. They also could detect no aggression between juveniles and adults of *Lemmus lemmus* in dyadic encounters in the field during a decline year. We need detailed information on the reproductive performance of individual female lemmings from all phases of the cycle.

Framstad, Stenseth & Østbye (Chapters 5 and 6, this volume) showed that not all peak years in *Lemmus lemmus* were accompanied by a curtailed summer breeding season. These comparisons for the Norwegian lemming are complicated by the shortage of data from years other than the peak of the cycle. More information on how individual Norwegian lemmings allocate reproductive effort in different cyclic phases is required.

MORTALITY IN LEMMINGS

Mortality parameters provide a second part of the demographic equation, but our knowledge of the age- and sex-specific mortality curves for lemmings is very poor. There is a shortage of detailed mark–recapture work on these rodents (see Jensen, Stenseth & Framstad, Appendix–chapter 2, this volume), and we know very little about the seasonal pattern of mortality.

Mortality rates during the winter are usually very low

No one has carried out mark–recapture through a winter so this generalization comes from observing the density in the autumn before snow and the density in spring as the snow melts. Because the lemming winter is so long, in the absence of reproduction numbers will fall dramatically even with an unusually high survival rate (e.g. > 0.9 per 2 weeks). There is of course no reason to expect a constant survival through all the winter. If there is normally a 'spring' breeding pulse under the snow in April, there could be a spring decline similar to that seen in other voles (Krebs & Boonstra, 1978). We do not know if this occurs or not. If a spring decline does occur, overwinter survival would have to be even higher to produce the observed numerical changes over the snowy season.

It is clear that in some but not all cyclic declines there is considerable winter mortality (e.g. Barrow 1949–1950, 1960–1961; Pitelka, 1973). But we do *not* know how these losses are distributed over the winter. They could occur primarily in the autumn (October) or be concentrated at the end of the snowy season (March–April) or during snow melt. It is important to remember that all the smooth curves drawn through the winter by Krebs (1964), Pitelka (1973) and others are extrapolations and are not measured population densities. Merritt (1984) has drawn together most of the information on the winter ecology of small rodents, and the shortage of demographic information in winter is highlighted by this book.

Juvenile mortality is especially high in peak and declining populations

This rule seems general for all fluctuating mammal and bird populations, although again there are few direct measurements for lemmings. The major question is why juvenile losses increase. The usual agents postulated are (1) predators, (2) food shortage, (3) social mortality (infanticide) and (4) disease.

Batzli *et al.* (1980) discuss an unpublished simulation model of *Lemmus* population dynamics at Barrow, Alaska, and they comment on the poor survival of juveniles that is an essential feature of the decline. Virtually everyone who has worked on cyclic rodents agrees that juvenile losses are a central feature of the cyclic syndrome, but there is no agreement on the mechanisms causing these losses.

Heske, Ims & Steen (Chapter 23, this volume) suggest that social mortality was not a factor in one summer decline of *Lemmus lemmus* in Norway, and they implicate predation as a major influence on survival. Since many predators fluctuate in synchrony with lemming populations, predation-based explanations of cyclic mortality patterns are very attractive. The question awaits an experimental attack.

Social interactions leading to mortality are an attractive explanatory agent because the same mechanism can be used to explain the curtailment of reproduction and the increase in juvenile losses in high density populations. The lemming cycle thus becomes a by-product of individual animals straining to increase their Darwinian fitness at all times. This mechanism of explaining cyclic changes is thus philosophically attractive, although empirically very uncertain for lemmings.

DISPERSAL

The importance of dispersal in rodent population dynamics has been shown by work on *Microtus* species almost entirely (reviewed in Lidicker, 1985). It is important to determine if lemmings are like *Microtus* in their dispersal strategy.

Presaturation dispersal is strong in cyclic and low density lemming populations

This conclusion is really more of a prediction because none of the relevant experimental work has been done yet on lemmings. If the *Microtus* pattern is followed by lemmings, they should follow the predictions given by Stenseth (1983). There is no evidence now to know if they do or not. Only anecdotal data are available.

Saturation dispersal at high densities may sometimes occur

Lemmings are known throughout the world for their 'migrations'. It is clear that there are local movements between adjacent habitats between winter and summer in some populations (Kalela & Koponen, 1971; see also Chapter 8, this volume). It is not clear that these local, individual movements ever become 'migrations' in the classic sense, or that individuals move over tens of kilometres. If long distance migrations occur, they are presumably good examples of non-adaptive dispersal (Stenseth, 1983), and we badly need to have mark–recapture work and radiotelemetry carried out on a local population before, during, and after a supposed migration.

What is striking is how migration is invoked in lemming ecology to explain anomalies in inadequate data sets. Pitelka (1973) gives one of the best examples of the *ad hoc* use of immigration to explain the peak *Lemmus* population of 1971 at Barrow, Alaska. I remain a sceptic on 'migrations'. We need mark–recapture and telemetry data. In addition, a population genetic approach could be useful to indicate spatial heterogeneity in gene frequencies. This approach could also suggest whether 'migrations' lead to homogenized genetic profiles of lemming populations. There has been virtually no work done on the ecological genetics of lemmings.

Brown lemmings at Barrow, Alaska shift habitats seasonally (Batzli, Pitelka & Cameron, 1983), as do Norwegian lemmings (Kalela *et al.*, 1971). Habitat use was not cycle-dependent, and all patterns of habitat use were linked to food availability, rather than protection from predators or increased snow insulation in winter (Batzli *et al.*, 1983). It is not known whether these results are general throughout the geographic range of the brown lemming.

FUTURE WORK

I have repeatedly observed that there is a shortage of demographic data from field populations of all the lemming species. There is a very good reason for this: lemming populations occur in remote areas and are difficult to study (Jensen, Stenseth & Framstad, Appendix–chapter 2, this volume). In view of this constraint, it is most important to decide on a priority list of what should be done next. Almost any lemming study would be useful, but a few would be critical. The following is my own list for future studies, worded as hypotheses that need testing.

The fence effect will occur very strongly in lemmings

In my opinion the fence experiment (Krebs, Keller & Tamarin, 1969) has produced the single most dramatic population effect of all the experiments done on field populations to date. I agree with Lidicker (1975, 1985) that the experimental procedure of frustrating dispersal is most instructive in unravelling the complexities of what causes populations to fluctuate.

The fence-effect, if it occurs in lemmings, points to *dispersal* as a key demographic element in population regulation. If dispersal – immigration and emigration – is not involved in population dynamics, the problem becomes a local one of site-specific factors affecting reproduction and survival. If the fence-effect occurs in lemmings, one can immediately conclude that social behaviour must form a large component of the explanation for lemming cycles. Attention can then be directed into a large number of lower order questions about the social biology of lemmings: for example, can related individuals recognize one another? Do adult females respond aggressively to unrelated juveniles? Do related animals breed in close proximity to one another? All these questions about social behaviour are interesting in themselves, but we need to determine if social behaviour has any direct consequences for population regulation.

There are technical difficulties in fencing a lemming population in winter. As a start, a summer fencing experiment itself would be useful, since the fence effect shows up very quickly in improved survival rates inside the fence (Krebs *et al.*, 1969, Boonstra & Krebs, 1977).

Heritability estimates for dominance, aggressiveness and dispersal tendency will be very high in lemmings

This prediction forms a critical test of some of the premises of the Chitty hypothesis (Krebs, 1978) and could be checked initially in laboratory populations. I suggest that this approach through quantitative genetics is more incisive than the technique of establishing breeding colonies from voles in different cyclic phases used by Hansson (1984a) and Gustafsson, Andersson & Westlin (1983). There is a great deal of natural selection that operates when any laboratory colony is established because not all individuals brought into the laboratory will breed. While we might hope that laboratory colonies of lemmings brought in from different cyclic phases are similar to those that occur in field populations in the same phase, this is at present only a great leap of faith.

Moss, Rothery & Trenholm (1985) have shown that dominance is strongly inherited in red grouse (*Lagopus lagopus*), and it would be useful to get similar data on lemmings. Boonstra & Boag (1987) have shown that cyclic populations of *Microtus pennsylvanicus* do not show any heritability of age at sexual maturity, growth rates, or body size, contrary to the predictions of the Chitty hypothesis. Experiments with laboratory populations of the Norwegian lemming have shown that there is a higher frequency of aggressive individuals at high density (Semb-Johansson, Wiger & Engh, 1979), but whether this is a purely phenotypic change is not known.

Female spacing behaviour is the critical determinant of recruitment rate in lemmings at all phases of the cycle

This prediction follows from work on *Microtus* summarized in Boonstra & Rodd (1983). Implicit in the prediction is the belief that social behaviour and social organization change over the cycle, and that infanticide is an important cause of juvenile losses in peak and declining populations of lemmings. There is a great deal of work waiting to be done here. I would begin by an experimental sex-ratio manipulation similar to that done by Hannon (1983). In *Dicrostonyx* these experiments could be used both to determine the role of adult female spacing behaviour in population dynamics and to help explain sex-ratio changes and the aberrant sex chromosome mechanisms in females (Fredga, 1983; see also Chapter 24).

Interspecific synchrony in cycles is caused by predation in the decline phase

If several species of small mammals live in the same general area, why should they all cycle in phase? Predation is the factor usually invoked to explain interspecific synchrony. This is an old hypothesis (Keith, 1963; Finerty, 1980) and there are two reasons for bringing it up again. First, it needs an experimental test in lemmings, and a predator-removal experiment during a lemming decline would be a valuable research project. Second, it should force us to analyse declines in much more detail. Do all vole and lemming species always decline exactly at the same time? Are they all equally profitable for predators to hunt? For many reasons the predation hypothesis is an attractive explanation for synchrony in vole and lemming declines (Henttonen *et al.*, 1984), but it will win no more adherents until experimental work is performed. Observations that predators rise and fall in numbers with the lemmings, and that predators eat a substantial fraction of the lemming population, are not evidence for the hypothesis that predation is necessary for synchronizing the decline phase in different species. Note that predation may *synchronize* the declines of different species without necessarily *causing* the declines.

CONCLUSIONS

There are two competing schools that attempt to explain the population dynamics of vertebrates (Caughley & Krebs, 1983). The first school believes that explanations for population changes should be sought in the predators, pathogens, parasites and food supply of the species involved. I call this the 'reindeer school' because it is typically used by large mammal ecologists who find it a sufficient model for most of the population changes they observe. In contrast, the second school believes that population changes cannot be understood without information on the social behaviour of the individuals making up the population. I call this the '*Microtus* school' because it evolved out of work on small rodents. I am a member of the second school, and the premise of this chapter has been that lemming population changes will be understood only when we have more information on their social behaviour.

There is much waiting to be done on the population biology of lemmings. I have tried in this chapter to apply to lemmings the details of the *Microtus*-cycle model that has evolved during the past 25 years from work done by many of us who believe that social behaviour and genetic changes must be a part of any final explanation of the mechanics of the lemming cycle.

There is an alternative view of lemming cycles enunciated by Pitelka (1973) and commonly adopted by the California school of small mammal workers (Lidicker, 1975, 1985) – the multifactorial approach. Each lemming cycle may have a different proximate explanation. I have criticized this view before (Krebs & Myers, 1974) but, like most paradigms, it is resistant to any empirical criticisms. What is important to me is to decide *what should we do next?* The experimental approach I suggest provides a list of critical experiments that need to be done. If there is one thing lacking in lemming population research over the past 25 years, it is the absence of an experimental paradigm. This is now coming and the next 25 years will see these problems largely solved.

Further progress in understanding lemming cycles will come by asking crisp experimental questions of field populations. This will not be easy. It is more convenient to work on temperate species like *Microtus* and *Clethrionomys*. We have, over the last 25 years, taken the lemming cycle south, analysed it in *Microtus* and obtained a working model. Now is the time to head back north and to determine whether lemmings are more like reindeer than like *Microtus*, or whether they are a unique case. I am betting they are large *Microtus*, not small reindeer.

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