Are lagomorphs similar to other small mammals in their population ecology?

C. J. KREBS

Department of Zoology, University of British Columbia, Vancouver, B.C., V6T 1W5, Canada

INTRODUCTION

The population biology of lagomorph mammals is a microcosm of population biology in general. In this paper I will review the current understanding of lagomorph population biology and try to compare it in a broad way with the paradigms that are emerging from the study of other small mammals, particularly the microtine rodents. I shall concentrate primarily on population dynamics in this paper, and therefore emphasize that this is only one part of lagomorph biology.

THEORY

Population biologists want to explain two general features of populations: (i) why they differ in average density from place to place, and (ii) why they do not grow exponentially. The theory of explaining these two features is simple (Krebs, 1985) but I repeat it here because it is still not understood by many ecologists.

To explain differences in average abundance, e.g., why Brown Hares (*Lepus europaeus*) are abundant on Swedish islands and not abundant on the adjacent mainland (Frylestam, 1979), one does *not* need to measure birth and death rates. In any stable population at *any* density:

births + immigration = deaths + emigration.

Thus if birth rates are lower on islands, death rates must also be lower. Consequently one should proceed by identifying a relevant *factor* and testing it experimentally.

To explain changes in abundance, e.g., why Brown Hares have been declining for the last 20 years in England (Tapper & Parsons, 1984), we need to measure birth, death, and migration rates to see why the imbalance occurs. The second step in explaining changes in abundance is controversial. One school suggests the experimental approach. The other school emphasizes *post hoc* analyses of mortality factors and their density dependence via key factor analysis. I clearly favour the first approach partly because the second approach has predominated for 50 years and has produced more heat than light.

I shall try to apply this simple theoretical framework to the detailed problems of lagomorph population dynamics and will attempt to convince you that it provides a good framework for analysis.

AVERAGE DENSITY

There are three general problems in lagomorph population dynamics that I classify as questions of average density–myxomatosis effects, island effects, and interspecific competition.

(1) Myxomatosis in Rabbits

The virus disease myxomatosis reduced the abundance of the Rabbit (*Oryctolagus cuniculus*) in Australia and throughout Western Europe and Britain during the early 1950s (Ross & Tittensor, 1986). There is no question but that this is the classic textbook example of successful biological control and the one feature of lagomorph population dynamics that is most widely known. It is also the most widely quoted example of host-disease co-evolution in the literature.

The great success of myxomatosis in reducing Rabbit numbers has produced two important questions: (i) is the myxomatosis–rabbit system inherently a stable equilibrium? (ii) if so, where is the stable point in relation to pest management needs? The first question cannot be answered because we do not have a realistic model of this disease system. Consequently, all we can do is adopt a look-and-see attitude (Ross & Tittensor, 1986). Rabbit populations seem to be rising gradually in much of central and southern England, although not in Wales, northern England, or Scotland (Trout *et al.*, 1986). We do not in fact know if this rise has anything to do with myxomatosis, and it is possible that changing agricultural practices are responsible instead. As one of the most significant practical problems in lagomorph ecology, it is most important that alternative hypotheses for this rise be developed and tested.

(2) Island effects

Both Mountain Hares and Brown Hares are much more abundant on islands off the Swedish coast where there are fewer predators (Frylestam, 1979; Lindlof & Lemnell, 1981). The relevant environmental variable to explain these island effects is usually assumed to be predator abundance and the mortality caused by predators must be partly additive to achieve these effects. The only other explanation for the island effect is that emigration is a source of loss on the mainland but not on islands. No one has tried to test the emigration hypothesis. Food resources seem to be worse on islands than on mainland sites, the opposite effect to what is needed to explain the average density differences. A quantitative analysis of these island effects is needed.

(3) Interspecific competition

In spite of the widespread belief that interspecific competition is a dominant force in community organization (Connell, 1983), there is almost no literature on interspecific competition in lagomorphs. There are rarely two species of lagomorphs present in the same habitat, and if competition is to be seen it will perhaps only be visible with more distantly-related herbivores like ungulates. The one exception seems to be the possible interaction between Brown Hares and Rabbits (Barnes & Tapper, 1986). I find the evidence unconvincing that the Rabbit reduction caused by myxomatosis released the Hare population to a higher average density because so much evidence is negative and several *ad hoc* assumptions must be added to explain the time sequences of bag data on which the tests are done. Whatever the truth of the matter, the effect of Rabbit reduction was transient and Brown Hare abundance is not readily understood by considering Rabbit abundance.

CHANGES IN ABUNDANCE

I will consider changes in abundance under two sub-headings: long-term trends, and population fluctuations.

(1) Long-term trends

Brown Hares have been declining in Britain and in Europe since about 1960 (Barnes & Tapper, 1986). The cause of this drop is unknown and could be due to climatic shifts or to agricultural changes. Long-term trends are very difficult to analyse experimentally and they require careful dissection to unravel. In theoretical terms, death and emigration rates must exceed birth and immigration rates, but the differences may be so slight as to be indetectable statistically. For example, a drop of 0·03 in annual survival of adult females would be sufficient to make a stable Hare population begin to decline about 5$^{0}_{0}$ per year. Without very large samples no one could detect such a minor change in survival amid all the noise of environmental variation.

I would suggest that we abandon any attempt to treat long-term trends as a dynamic problem by measuring rates of birth and death. We should treat them as average-density problems and measure only the density changes involved, coupled with experimental analysis if possible. For the Brown Hare this would mean trying to identify and manipulate specific agricultural parameters to see if the density trends are reversed. Long-term observations are clearly at the heart of analysing long-term trends, and there is no easy road to resolution. We cannot manipulate weather, if it is the suspected factor, but by identifying the specific effects of weather (on reproduction, on juveniles, etc.) we may be able to provoke specific tests of weather hypotheses.

The preceding argument is one reason why I have treated the most crucial long-term lagomorph trend of the century—the recovery of Rabbit populations after myxomatosis—in the section on average density. Most emphatically, the recovery of Rabbit populations can never be explained by observations on the fraction killed by the current myxomatosis virus strain, and the simple equation that:

$$\begin{array}{ccc} \text{more resistant} + & \text{less virulent} & = \text{increasing Rabbit} \\ \text{rabbits} & \text{virus} & \text{populations} \end{array}$$

is demographically dubious. It assumes that all myxomatosis mortality is additive, and there is no evidence at present that it is (although clearly it was additive in the early 1950s). How could we test the assumption that present-day myxomatosis mortality is additive? One approach is to immunize a natural Rabbit population so that there is no myxomatosis effect and see whether numbers rise. Sobey, Conolly & Westwood (1983) have already done this experiment at Lake Urana, N.S.W., but the results are not yet published.

One elegant experiment on the additivity of mortality has been reported by Williams (1985). In New Zealand, Rabbits exist at low densities in fertile grazing farmland. Shooting was carried out over 5 years on one site and an unmanipulated area was counted nearby. Shooting mortality did not affect annual density trends or average density on the two farms, primarily because it affects only adult mortality and is not additive but compensatory to other forms of mortality. Juvenile mortality factors are responsible for population trends, and these are being investigated.

Whether mortality factors are additive or compensatory is one of the most pressing and most difficult questions in mammalian ecology. Lagomorph ecologists can make an important contribution to its resolution by careful experimentation.

(2) Fluctuations and cycles

Both Rabbit and Hare populations fluctuate in size on a scale large enough to analyse by measuring birth and death rates. Keith (1981, 1983) has recently reviewed much of this literature for Hares, but there is no comparable review for Rabbits. Keith (1983)

has pointed out that the Mountain Hare in the boreal forest of the U.S.S.R. fluctuates in 9–10 year cycles like the Snowshoe Hare in North America. I will not discuss the Snowshoe Hare cycle here, since this has been thoroughly covered in other papers. Three European species are however of interest.

The Mountain Hare (*Lepus timidus*) is reported to fluctuate in short-term (3–4 year), low amplitude (less than 10 : 1), cycles in northern Fennoscandia (Hornfeldt, 1978; Pulliainen, 1982; Angelstam *et al.*, 1984). These fluctuations are currently under study by Lindstrom *et al.*, (1986) who are testing the hypothesis that predators limit Hare populations, and the cycle is imposed on Hares by a shift of generalist predators from microtine rodents during their cyclic decline and low phases. Correlative evidence gathered to date is supportive (Angelstam *et al.*, 1984) and the critical manipulative experiments are now under way. The alternative hypothesis is that these short cycles in Mountain Hares are food-driven but this is deemed unlikely by Keith (1983).

Rabbit populations in Britain clearly fluctuate but I have nowhere seen a clear statement why. The unwritten consensus seems to be that many factors are involved in year-to-year fluctuations, and ecologists are divided as to whether they regard this multifactor model as the quintessence of truth (Lidicker, 1985) or the product of sloppy thinking (Krebs & Myers, 1974).

Food limitation is one factor that may be invoked to explain fluctuations in Rabbit numbers. Garson (1986) has reported experimental work to test this hypothesis at Holy Island. Parer (1977) suggested for Australia that food supplies were critical to Rabbits only before myxomatosis occurred, and that now predators are likely most important. Cooke (1981) describes a Rabbit population in arid Australia that shows typical Andrewartha-and-Birch dynamics in response to food availability, which is largely rainfall dependent. Gibb (1981) has argued that New Zealand Rabbit populations are limited by food shortage interacting with predation. There is a danger in accepting multifactor hypotheses like these on simple observational evidence, as Gibb (1981) has done, without the experimental verification that could come from 2- or 3-factor manipulative designs.

Almost no one seems to feel that social behaviour is of any consequence for understanding population limitation in Rabbits. Parer (1977) stated that the Rabbit has no effective intrinsic mechanism of population control. Only Henderson (1979) argues otherwise for a possible spacing behaviour model of population limitation in Rabbits. One of the oddest features of lagomorph biology to an outsider is that Rabbit social behaviour has been studied so much and has become a model system in behavioural biology, while at the same time none of these studies has been directed toward population dynamics. The implicit conclusion is that social behaviour has no impact whatever on population dynamics. But all this has been concluded without a single attempt to apply the Watson & Moss (1970) model to Rabbits, a situation I find quite astonishing in view of all the work that has been done on Rabbits.

It is true that the Rabbit is an introduced species in most of its current geographical range, and consequently we could use Chitty's (1960) admonition that any self-regulatory system has evolved to operate in a restricted range of environments and will not operate everywhere in all populations, to support Gibb's (1981) contention that social behaviour is irrelevant to population limitation in the Rabbit in New Zealand. But this is an empirical question that can be answered only by doing the relevant studies.

To summarize, the emerging paradigm of population limitation in the Rabbit is a multifactor model of food shortage and predation, possibly aggravated by diseases and parasites.

It is interesting to ask why populations of Rabbits and Brown Hares (Tapper & Parsons, 1984) do not show population cycles such as those which occur in *Lepus timidus* in Scotland (Hewson, 1976) and the U.S.S.R. (Keith, 1983) and in *Lepus americanus* in North America. Keith (1983) argues that cycles can occur only when habitats are continuous, and that once favorable habitat becomes island-like, lagomorphs are regulated by dispersal losses between habitat-blocks. Richards (1985) supports the same model to explain cyclic and non-cyclic populations of *Microtus agrestis* in England. This model is reasonable but completely untested. We know nothing about the survival rate of dispersing lagomorphs in patchy environments in relation to survival within patches. We do not have a quantitative analysis of patch size and interpatch distances in relation to lagomorph dynamics to make this vague model more precise.

One alternative hypothesis is that cyclic populations have different social structure from non-cyclic populations (Bell & Cowan, 1986). This would seem unlikely even from our limited knowledge. For example, the non-cyclic Brown Hare has a social system based on dominance hierarchies (Holley, 1986) that seems identical to the social system in the cyclic Snowshoe Hare (Graf, 1985).

The simplest models of populations (Krebs, 1985, p. 210) suggest that in a mathematical world cyclicity will be favoured when either (i) carrying capacity is larger or (ii) the population growth rate falls more rapidly as density is increased. Thus in poor habitats where resources are low, cycles should not occur. This prediction could be checked empirically. It is more difficult to understand condition (ii) in a mechanistic sense. No one has checked prediction (ii); if it is correct, the birth, death and movement mechanisms must still be specified. There are data from the Snowshoe Hare and the Mountain Hare to do these calculations, but I have not found adequate data for the Brown Hare. Figure 1 shows the relationship between net reproductive rate and population density for the Snowshoe Hare and the Mountain Hare. If we define L as the absolute value of the slope of the regression times the equilibrium density (Krebs, 1985), then we get these results from Fig. 1:

	Slope	Equilibrium density/100 ha	L
Snowshoe Hare			
Rochester	0·005	340	1·7
Kluane	0·010	300	3
Mountain Hare			
Scotland	0·050	40	2

All these values of L are in the range expected for oscillations to occur. It would be interesting to have comparable data from the Brown Hare to see if L is 1 or less and stable populations would be predicted. The problem with this, as with all simple models, is that we do not know from this analysis exactly what factors cause population growth to decrease at high densities. The only useful message from Fig. 1 is that low density *per se* (as in Mountain Hares in Scotland) is not sufficient to prevent cycling (as Hewson, 1976 has recognized).
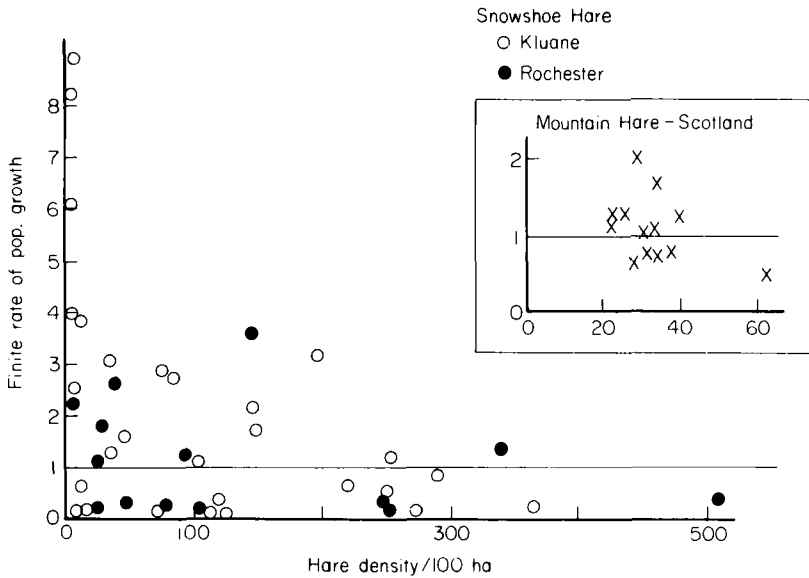
Fig. 1. Finite rate of population growth per year (N_{t+1}/N_t) in relation to population density at the start of the year (1 April) for two populations of Snowshoe Hares from Canada and one population of Mountain Hares from Scotland. Rochester data from Cary & Keith (1979), Yukon data from our unpublished data, and Scotland data from Hewson (1976).

CONTROL OF REPRODUCTION

The length of the breeding season in both Hares and Rabbits is believed to be largely controlled by daylength (Keith, 1981; Boyd, 1986). Boyd (1986) has detailed a model of how daylength controls the breeding of the Rabbit. I would suggest that the day-length model of seasonal breeding has been a positive hindrance to our understanding of the ecology of reproduction in wild lagomorphs. It ignores the evolutionary forces behind the timing of breeding seasons, with the result (for example) that in arid Australia Rabbits may breed all year or only for 2 months, depending on rainfall and plant growth (Cooke, 1981). The daylength model may provide a broad background but the critical variations that occur in the length of breeding seasons are more properly analysed as products of social behaviour or food shortage. It is these variations that interest the population biologist trying to understand population dynamics.

There is considerable evidence for the Rabbit that social behaviour can affect physiological states (Bell, 1986) but we do not know if these social effects have popula-tion consequences. Cowan & Garson (1985) have shown that scramble competition for food in sand dune habitat causes greater density fluctuations in Rabbits than occur in chalk downland where there is contest competition for burrows and mates. This seems to be a clear case where habitat features dictate social organization and population dynamics. What we do not know is whether fluctuations in density within a habitat can be produced by social processes involving dominance and aggressive behaviour. Gibb (1981) does not believe this is possible, and it would certainly be a minority view to suggest otherwise.

CONCLUSION

To answer the question with which I began, *no*, lagomorphs apparently are not similar to other small mammals in their population ecology. They violate the paradigm

enunciated by Caughley & Krebs (1983) that small mammal populations are self-regulated. In their overall dynamics—cycles, irregular fluctuations, island effects—they are similar to voles and lemmings, but the mechanisms responsible for these changes are thought to be predation, food shortage, and possibly disease. There is no suggestion that social behaviour plays a role in the population dynamics of Rabbits or Hares, as it seems to in voles and lemmings. This could be a correct perception, or it could be a reflection of the failure to analyse lagomorph populations as groups of individuals, each intent on maximizing its own fitness. One missing piece of lagomorph research is work on the population consequences of individual differences in genetics, physiology, and behaviour. If there is an agenda for lagomorph research for the next 10 years, I hope two items are 'writ large': the analysis of individual differences in relation to population dynamics, and the experimental testing of our present hypotheses.

ACKNOWLEDGMENTS

REFERENCES

Angelstam, P., Lindstrom, E., & Widen, P. (1984) Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia, 62,* 199–208.
Barnes, R. F. W. & Tapper, S. C. (1986) Consequences of the myxomatosis epidemic in Britain's Rabbit (*Oryctolagus cuniculus* L.) population on the numbers of Brown Hares (*Lepus europaeus* Pallas). *Mammal Review,* 16, 111–116.
Bell, D. J. (1986) Social effects on physiology in the European Rabbit. *Mammal Review,* 16, 131–137.
Boyd, I. L. (1986) Effect of daylength on the breeding season in male Rabbits. *Mammal Review,* 16, 125–130.
Cary, J. R. & Keith, L. B. (1979) Reproductive change in the 10-year cycle of snowshoe hares. *Canadian Journal of Zoology, 57,* 375–390.
Caughley, G. & Krebs, C. J. (1983) Are big mammals simply little mammals writ large? *Oecologia, 59,* 7–17.
Chitty, D. (1960) Population processes in the vole and their relevance to general theory. *Canadian Journal of Zoology, 38,* 99–113.
Connell, J. H. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist, 122,* 661–696.
Cooke, B. D. (1981) Food and dynamics of rabbit populations in inland Australia. *Proceedings of the World Lagomorph Conference.* (Ed. by K. Myers & C. D. MacInnes), pp. 633–647. University of Guelph, Ontario.
Cowan, D. P. & Bell, D. J. (1986) Leporid social behaviour and social organization. *Mammal Review,* 16, 169–179.
Cowan, D. P. & Garson, P. J. (1985) Variations in the social structure of rabbit populations: causes and demographic consequences. *Behavioural Ecology.* (Ed. by R. M. Sibley & R. H. Smith). pp. 537–555. Blackwell Scientific Publications, Oxford.
Frylestam, B. (1979) Studies on the European hare. XXXV. Structure, size, and dynamics of three European hare populations in southern Sweden. *Acta Theriologica, 24,* 449–464.
Garson, P. (1986) Food limitation of a Rabbit population: observational and experimental evidence from a study in coastal duneland habitat. *Mammal Review,* (in press).
Gibb, J. (1981) Limits to population density in the rabbit. *Proceedings of the World Lagomorph Conference.* (Ed. by K. Myers & C. D. MacInnes), pp. 654–663. University of Guelph, Ontario.
Graf, R. (1985) Social organization of snowshoe hares. *Canadian Journal of Zoology, 63,* 468–474.
Henderson, B. A. (1979) Regulation of the size of the breeding population of the European rabbit. *Oryctolagus cuniculus,* by social behaviour. *Journal of Applied Ecology,* 16, 383–392.
Hewson, R. (1976) A population study of mountain hares (*Lepus timidus*) in north-east Scotland from 1956–1969. *Journal of Animal Ecology, 45,* 395–414.
Holley, A. J. F. (1986) A hierarchy of Hares: dominance status and access to oestrous does. *Mammal Review,* 16, 181–186.
Hornfeldt, B. (1978) Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. *Oecologia, 32,* 141–152.
Keith, L. B. (1981) Population dynamics of hares. *Proceedings of the World Lagomorph Conference.* (Ed. by K. Myers & C. D. MacInnes). pp. 395–440. University of Guelph, Ontario.
Keith, L. B. (1983) Role of food in hare population cycles. *Oikos, 40,* 385–395.
Krebs, C. J. (1985) *Ecology: The Experimental Analysis of Distribution and Abundance.* 3rd. edn. Harper and Row, New York.

Krebs, C. J. & Myers, J. H. (1974) Population cycles in small mammals. *Advances in Ecological Research,* **8,** 267–399.

Lidicker, W. Z. J. (1985) Population structuring as a factor in understanding microtine cycles. *Acta Zoologica Fennica,* **173,** 23–27.

Lindlof, B. & Lemnell, P. A. (1981) Differences in island and mainland populations of mountain hare. *Proceedings of the World Lagomorph Conference.* (Ed. by K. Myers & C. D. MacInnes), pp. 478–485. University of Guelph, Ontario.

Lindström, E., Andrén, H., Angelstam, P. & Widén, P. (1986) Influence of predators on Hare populations in Sweden: a critical review. *Mammal Review,* **16,** 151–156.

Parer, I. (1977) The population ecology of the wild rabbit, *Oryctolagus cuniculus* (L.), in a Mediterranean-type climate in New South Wales. *Australian Wildlife Research,* **4,** 171–205.

Pulliainen, E. (1982) Habitat selection and fluctuations in numbers in a population of the arctic hare (*Lepus timidus*) on a subarctic fell in Finnish forest Lapland. *Zeitschrift für Saugetierkunde,* **47,** 168–174.

Richards, C. G. J. (1985) The population dynamics of *Microtus agrestis* in Wytham, 1949 to 1978. *Acta Zoologica Fennica,* **173,** 35–38.

Ross, J. & Tittensor, A. M. (1986) Influence of myxomatosis in regulating Rabbit numbers. *Mammal Review,* **16,** 163–168.

Sobey, W. R., Conolly, D. & Westwood, N. (1983) Myxomatosis: a search for a strain of virus to immunize a wild population of rabbits, *Oryctolagus cuniculus. Australian Wildlife Research,* **10,** 287–295.

Tapper, S. & Parsons, N. (1984) The changing status of the Brown hare (*Lepus capensis* L.) in Britain. *Mammal Review,* **14,** 57–70.

Trout, R. C., Tapper, S. C. & Harradine, J. (1986) Recent trends in the Rabbit population in Britain. *Mammal Review,* **16,** 117–123.

Watson, A. & Moss, R. (1970) Dominance, spacing behavior and aggression in relation to population limitation in vertebrates. *Animal Populations in Relation to Their Food Resources.* (Ed. by A. Watson), pp. 167–220. Blackwell Scientific Publications, Oxford.

Williams, J. M. (1985) The dynamics of managed European rabbit populations on New Zealand pastoral farmland. *IV International Theriological Congress,* Edmonton, Canada, August 1985.