

WHAT DETERMINES THE NUMBERS OF SMALL HERBIVOROUS MAMMALS?

JOHN A. GIBB

Ecology Division, DSIR, Lower Hutt

SUMMARY: This paper considers the questions of what limited peak density, and what caused the long decline after peak density, in a confined population of wild rabbits, *Oryctolagus cuniculus*. An hypothesis is proposed in which both food shortage and predation are essential components. This may also be relevant to free-living populations of voles, lemmings, and perhaps other small herbivorous mammals.

EARLY CONFLICTS

Fifteen years ago Elton (1966) remarked that the "whole field of population control in nature and theories about how it works has got into a rather peculiar state". Population ecologists were arrayed in two main opposing camps: some stressed the immediate importance of extrinsic factors such as food shortage, predation and disease in determining animal numbers, while others supposed that animals limit their own density by some form of territorial behaviour that spaces them out and more or less assures the successful ones of an adequate supply of the resources they need.

The periodic fluctuations in numbers of voles and lemmings, and of snowshoe hares (*Lepus americanus*), have attracted attention for many years; indeed Elton (1942) defined many of the problems that still worry population biologists today. Lack (1954) argued strongly that food shortage was the one effective and ubiquitous factor limiting the size of animal populations. He was supported by Pitelka (e.g. 1958) working with voles and lemmings; while more recently Batzli *et al.* (1980) have been specially concerned with the nutritional quality of food rather than with its gross amount or calorific value.

The simplicity of the food hypothesis (Fig. 1) was appealing, but Chitty (e.g. 1955, 1958) and Krebs (1964) pointed out that voles and lemmings often decline in numbers without actually exhausting the food supply; in fact they are usually in good condition at peak density and rarely seem to starve or suffer obvious nutritional disorders. Succumbing to this "illusion of plenty" (Jones, 1979), Chitty and others (e.g. Wynne-Edwards, 1962) denied the immediate importance of food shortage simply because the effects of grazing were not always obvious and it may look as if there is plenty of food left. Similarly Krebs did not believe that his lemmings were short of food at peak density, though they may have consumed up to about 24% of the

standing vegetation (Krebs, 1964, his Table 38). This may not seem a very high figure; but Batzli and Pitelka (1970, 1971) have pointed out that not all vegetation is suitable as food and that at high density voles often severely deplete the supply of their preferred foods. This may make it difficult for them to secure a properly balanced diet without exposing themselves to predation, as happens to rabbits and other animals (Gibb, Ward and Ward, 1978; Jones, 1979).

Krebs (1964) was probably correct in rejecting food shortage as a complete answer to what limits

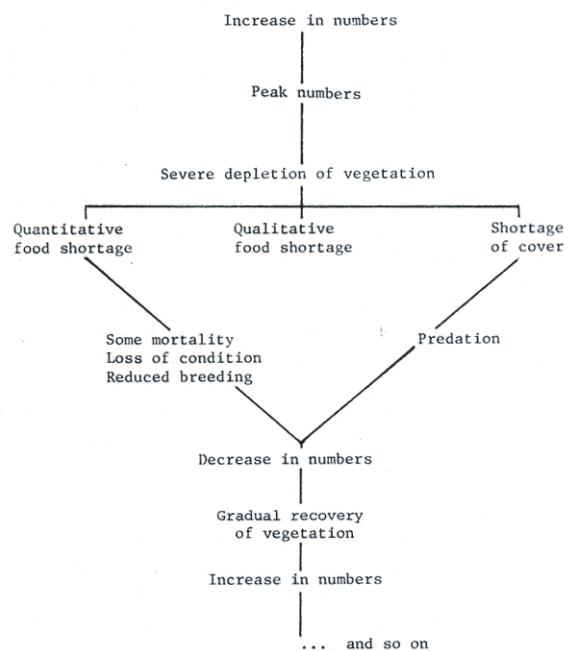


FIGURE 1. Pitelka's food-supply hypothesis. (After Krebs, 1964.)

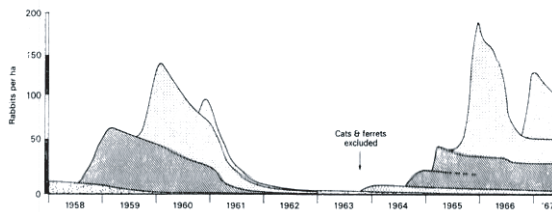


FIGURE 2. Density of rabbits in an 8.5 ha enclosure from 1958 to 1967, showing survival of annual cohorts. Feral cats and mustelids had free access until October 1963, but thereafter most were excluded.

density, but it may still be important - perhaps combined with other factors. Having earlier also rejected food shortage as well as predation on what now seem rather shaky grounds, Chitty (1958, see also Krebs, 1978) propounded his hypothesis of genetic changes in the quality of the animals to explain the observed fluctuations in numbers.

At that time Krebs (1971) adhered to the single-factor approach to population regulation, and wrote: "If you believe that food shortage is the most important resource involved, you must view these genetic experiments as meaningless. . . if you believe that predation is the driving force, you would view food shortage experiments as meaningless". Lidicker (1973, 1978) warned of the danger of examining single factors one at a time and rejecting each as inadequate, when the real answer lies in an interaction between two or more of them.

A CONFINED POPULATION OF RABBITS

A major difficulty in studying animals as small as voles or lemmings, often in dense vegetation, is that they cannot be watched; whereas rabbits can be watched and counted when above ground. We (Gibb, 1977; Gibb *et al.*, 1971:1; Gibb, in press) watched our rabbits (*Oryctolagus cuniculus*) in an enclosure of 8.5 ha for 10 years spanning two population "cycles" (Fig. 2). Natural predators had free access during the first cycle, but in the second most of the carnivores (feral cats and ferrets) were experimentally excluded.

The same two questions arose with the rabbits as with voles and lemmings, namely what limited peak density and what caused the long decline after the first peak? With other biologists of the day we sought to identify which one of the suggested limitations to population size was effective. It was only after the study was over that we realised that what we had seen in our rabbits might shed some light on hidden facets of microtine ecology.

Food shortage stopped further breeding at both population peaks. As usual the pasture dried out in summer, but in peak years the rabbits kept it grazed to the ground through the following autumn and winter as well. However, food shortage does not necessarily imply starvation. During the first peak a few young rabbits may have starved and others certainly died of coccidiosis; while young born late in the season grew much more slowly and survived much less well than those born earlier, which did not happen at lower densities. Adult rabbits, on the other hand, lost very little weight in summer and survived both periods of peak density very well: their heaviest mortality came later in the year.

Since the size of both peaks was limited primarily by food shortage, as Lidicker (e.g. 1978) postulated for *Microtus*, they reached roughly similar densities. The maximum density in the second peak, without carnivores, was slightly higher than in the first, but it was very short-lived.

With food shortage becoming increasingly acute after the first peak, the rabbits risked predation to get enough. They spent longer out above ground foraging, instead of resting more securely underground; they had to forage further from the warrens, and they became less alert. Consequently, first the young of the year and then the older rabbits fell prey to the cats and ferrets; and for three successive breeding seasons no young survived for more than a week or two after leaving the nest.

Eventually, 3t years after peak density, only 11 males and 2 females survived - from the original 1000 rabbits. Then we removed the carnivores. This immediately allowed young to survive, stopped the decline, and led to the second peak two years later.

After this second peak, with most carnivores still excluded, food shortage soon turned into outright starvation. Once again, the young died first and older cohorts later; and many more males died than

females. Some full grown rabbits lost about half their body weight before dying, while others survived weight losses of 40-50%.

DISCUSSION

Population control

Our study 'suggested a revision of Pite1ka's original food hypothesis, with food shortage still playing its central part but resulting variously in increased mortality from starvation, predation, or disease (Fig. 3).

The rabbits' behaviour did not prevent their exhausting the food supply. Though confined populations may be more liable to exhaust their food than are free-ranging ones (Krebs, 1971), many wild populations of rabbits that happen to be exempt

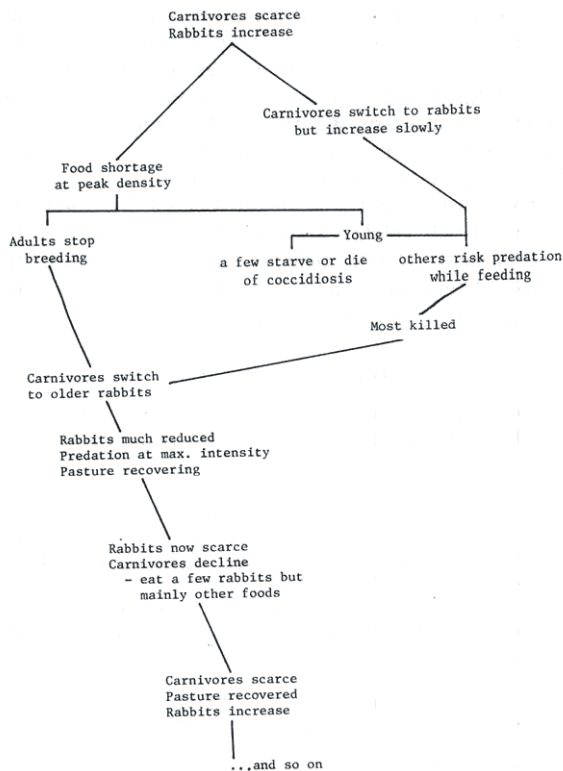


FIGURE 3. Proposed hypothesis involving both food shortage and predation.

from heavy predation seem to live more or less permanently close to the food limit (pers. observation). Thus the rabbits' behaviour seemed more effective in deciding which ones survived, than how many. Genetic changes in the population cannot have accounted for the change from increasing to decreasing numbers (cf. Chitty, 1955), as the rabbits which survived the decline were the same ones as had earlier contributed most to the peak.

The early stages of the rabbits' first decline were accelerated as much by the carnivores switching to feed on rabbits as by their increased numbers; and this was aided by the rabbits exposing themselves to predation in response to food shortage at high density. However, the carnivores went on reducing the numbers of rabbits, though at a much reduced rate, long after the pasture had substantially recovered and when the rabbits were no longer short of food. The nutrient-recovery hypothesis of Schultz (1964) was therefore inapplicable.

Some cats survived during the later stages of the rabbits' decline by eating mainly other foods, and so reduced the numbers of rabbits much lower than

if there had been nothing else for them to eat - when they would have starved. The availability of other foods for the carnivores thus had the effect of exaggerating the rabbits' decline.

This differs from Errington's (1963) view that predators confine their attention to biologically expendable parts of prey populations: for, as with Pearson's (1966) voles, "the carnivores were catching not just the sick, homeless and maladjusted; they caught almost everyone". On the other hand, our situation may resemble Caughley *et al.*'s (1980) interpretation of dingo (*Canis familiaris*) predation which, they suggest, may mice have limited the density of red kangaroos (*Megaleia rufa*), while the numbers of dingoes were "determined not by the abundance of kangaroos but by that of a suite of smaller prey species".

Although a long decline such as we saw in the rabbits is to be expected in a predator-prey interaction (Lack, 1954, p. 214), Chitty (1967) referred to the, characteristically long decline of voles and lemmings after peak density as "their most puzzling feature". Neither he, nor Lack (1954), Pitelka, Tomich and Treichel (1955), or Krebs (1964) attributed the decline to predation.

Yet when Pearson (1966, 1971) found that house cats accounted for a crash in the numbers of *Microtus californicus*, he predicted that carnivore predation would be found responsible for the amplitude and timing of the microtine cycle: "no carnivores, no cycle" (Pearson, 1966), or more specifically with *M. montanus* in the Sierra Nevada, "no weasels, no cycle" (Fitzgerald, 1977). Pitelka (1973) has now accepted this key role of carnivores in the cycle.

The interaction between the rabbits and their food supply, and then with the carnivores, generated a 'predator-prey' cycle - though food and predators were both essential to it (Fig. 4). Similarly the 10-year cycle of snowshoe hares is apparently generated first by their being short of food in winter, which initiates the decline, and then by their interaction with the lynx, which prolongs and deepens it (Keith *et al.*, 1977; Keith and Windberg, 1978).

In some regions, as in Alaska, the decline of the hares may be accentuated because they cannot eat the new growth of arctic willows (*Salix* spp.), which they induce by consuming the mature leaves. The root suckers are protected by specially high concentrations of resin, which make the leaves unpalatable or even toxic (Bryant, in press; McKey, 1974). Other food plants elsewhere may similarly mobilise chemical defences which may affect the numbers of herbivores.

The fence effect

Free-ranging populations of rabbits in New Zealand or elsewhere rarely fluctuate as ours did. Confined populations of rabbits, as of voles, are presumably subject to the "fence effect" (Krebs, 1971), which exaggerates their fluctuations. At least in the short term, many low-density wild populations of rabbits are fairly stable, probably restrained below the food limit by predation (Gibb *et al.*, 1969; Gibb, unpubl.); and it is mainly in confinement or on small islands (Watson, 1961), or in specially erratic environments as in parts of Australia, that they fluctuate widely. The way populations of rabbits behave is evidently less a property of the animals themselves than of the situations in which they live.

CONCLUSION

While sympathising with Watson and Moss (1970) and Krebs *et al.* (1973) in looking for some common explanation of animal population control, we must always allow for the mix of controlling factors to vary between species, populations of the same species, and through time (Ehrlich and Birch, 1967). From experience with birds and mammals I am impressed with the overwhelming importance, not of

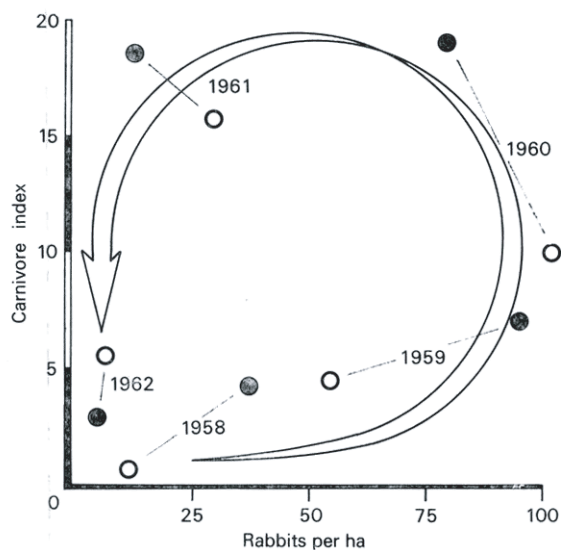


FIGURE 4. Relationship between the density of rabbits and the frequency with which the carnivores were seen, during the period when cats and mustelids had free access to the 8.5 ha study area. Open circles (o) indicate plots for autumn-winter, closed circles (●) for spring-summer. (After Gibb *et al.*, 1978).

starvation as a mortality factor, but of varying degrees of food shortage in predisposing animals to mortality from a variety of causes. Exact identification of these immediate causes of mortality may be rather unimportant (Chitty, 1961; Krebs, 1978); it will certainly be counter-productive if it distracts from discovering the ultimate causes.

An holistic approach as advocated by Lidicker (1978), which relates the animal's behaviour to its environment, should help to identify the mix of factors determining animal numbers and to see how the regulatory process works.

ACKNOWLEDGEMENTS

I thank Des B. M. Fitzgerald and J. E. C. Flux for useful discussion and criticism of this manuscript.

REFERENCES

- BATZLI, G. O.; PITELKA, F. A. 1970. Influence of meadow mouse populations on California grassland. *Ecology* 51: 1027-39.
- BATZLI, G. O.; PITELKA, F. A. 1971. Condition and diet of cycling populations of the California vole *Microtus californicus*. *Journal of Mammalogy* 52: 141-63.
- BATZLI, G. O.; WHITE, R. G.; MACLEAN, S. F. JR.; PITELKA, F. A.; COLLIER, B. D. 1980. The herbivore-based trophic system. In: Brown, J.; Miller, P. C.; Tieszen, L. L.; Bunnell, F. L. (Editors). *An Arctic Ecosystem: the Coastal Tundra at Barrow, Alaska*. US/IBP Synthesis Series 12: 335-410. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.
- BRYANT, J. P. in press. The regulation of snowshoe hare feeding behaviour during winter by plant anti-herbivore chemistry. *Proceedings of the World Lagomorph Conference. 13-17 August 1979, Guelph*.
- CAUGHLEY, G.; GRIGG, G. C.; CAUGHLEY, J.; HILL, G. J. E. 1980. Does dingo predation control the densities of kangaroos and emus? *Australian Wildlife Research* 7: 1-12.
- CHITTY, D. 1955. Adverse effects of population density upon the viability of later generations. In: Cragg, J. B.; Pirie, N. W. (Editors). *The Numbers of Man and Animals*. Institute of Biology Symposium 4: 57-67. Oliver and Boyd, Edinburgh.
- CHITTY, D. 1958. Self-regulation of numbers through changes in viability. *Cold Spring Harbor Symposium of Quantitative Biology* 22: 277-80.
- CHITTY, D. 1961. Review of "The Lifespan of Animals". Wolstenholme, G. E. W.; O'Connor, M. (Editors). Churchill, London, 1959. *Journal of Animal Ecology* 30: 189.
- CHITTY, D. 1967. The natural selection of self-regulatory behaviour in animal populations. *Proceedings of the Ecological Society of Australia* 2: 51-78.
- EHRlich, P. R.; BIRCH, L. C. 1967. The "balance of nature" and "population control". *American Naturalist* 101: 97-107.

- ELTON, C. S. 1942. *Voles, Mice and Lemmings: Problems in Population Dynamics*. Oxford University Press, London. 496 pp.
- ELTON, C. S. 1966. *The Pattern of Animal Communities*. Methuen, London. 432 pp.
- ERRINGTON, P. L. 1963. The phenomenon of predation. *American Scientist* 51: 180-92.
- FITZGERALD, B. M. 1977. Weasel predation on a cyclic population of the montane vole (*Microtus montanus*) in California. *Journal of Animal Ecology* 46: 367-97.
- GIBB, J. A. 1977. Factors affecting population density in the wild rabbit, *Oryctolagus cuniculus* (L.), and their relevance to small mammals. In: Stonehouse, B.; Perrins, C. M. (Editors). *Evolutionary Ecology*. pp. 33-46. Macmillan, London.
- GIBB, J. A. in press. Limits to population density in the rabbit, *Oryctolagus cuniculus* (L.). *Proceedings of the World Lagomorph Conference, 13-17 August 1979, Guelph*.
- GIBB, J. A.; WARD, C. P.; WARD, G. D. 1978. Natural control of a population of rabbits, *Oryctolagus cuniculus* (L.), for ten years in the Kourarau enclosure. *New Zealand Department of Scientific and Industrial Research Bulletin* 223: 1-89.
- GIBB, J. A.; WARD, G. D.; WARD, C. P. 1969. An experiment in the control of a sparse population of wild rabbits (*Oryctolagus cuniculus* (L.)) in New Zealand. *New Zealand Journal of Science* 12: 509-34.
- JONES, R. 1979. Predator-prey relationships with particular reference to vertebrates. *Biological Review* 54: 73-97.
- KEITH, L. B.; TODD, A. W.; BRAND, C. J.; ADAMCIK, R. S.; RUSCH, D. H. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. In: Peterle, T. J. (Editor). *XIIIth International Congress of Game Biologists. Atlanta, Georgia, U.S.A., March 11-15, 1977*. pp. 151-75. Washington, D.C.
- KEITH, L. B.; WINDBERG, L. A. 1978. A demographic analysis of the snowshoe hare cycle. *Wildlife Monographs* 58: 1-70.
- KREBS, C. J. 1964. The lemming cycle at Baker Lake, Northwest Territories, during 1959-62. In: Britton, M. E. (Editor). *Alaskan Arctic Tundra*. Arctic Institute of North America, Technical Paper No. 15: 1-104.
- KREBS, C. J. 1971. Genetic and behavioural studies on fluctuating vole populations. *Proceedings of the Advanced Study Institute on 'Dynamics of numbers in populations', Oosterbeek 1970*: 243-56.
- KREBS, C. J. 1978. A review of the Chitty Hypothesis of population regulation. *Canadian Journal of Zoology* 56: 2463-80.
- KREBS, C. J.; GAINES, M. S.; KELLER, B. L.; MYERS, J. H.; TAMARIN, R. H. 1973. Population cycles in small rodents. *Science* 179: 35-41.
- LACK, D. 1954. *The Natural Regulation of Animal Numbers*. Oxford University Press, London. 280 pp.
- LIDICKER, W. Z. 1973. Regulation of numbers in an island population of the California vole, a problem in community dynamics. *Ecological Monographs* 43: 271-302.
- LIDICKER, W. Z. JR. 1978. Regulation of numbers in small mammal populations - historical reflections and a synthesis. In: Snyder, D. P. (Editor). *Populations of small mammals under natural conditions*. pp. 122-66. Pymatuning Laboratory of Ecology, University of Pittsburg.
- McKEY, D. 1974. Adaptive patterns in alkaloid physiology. *American Naturalist* 108: 305-20.
- PEARSON, O. P. 1966. The prey of carnivores during one cycle of mouse abundance. *Journal of Animal Ecology* 35: 217-33.
- PEARSON, O. P. 1971. Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). *Journal of Mammalogy* 52: 41-49.
- PITELKA, F. A. 1958. Some aspects of population structure in the short-term cycle of the brown lemming in northern Alaska. *Cold Spring Harbor Symposium of Quantitative Biology* 22: 237-51.
- PITELKA, F. A. 1973. Cyclic pattern in lemming populations near Barrow, Alaska. In: Britton, M. E. (Editor). *Alaskan Arctic Tundra*. Arctic Institute of North America, Technical Paper No. 25: 199-215.
- PITELKA, F. A.; TOMICH, P. Q.; TREICHEL, G. W. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. *Ecological Monographs* 25: 85-117.
- SCHULTZ, A. M. 1964. The nutrient-recovery hypothesis for arctic microtine cycles. 2. Ecosystem variables in relation to arctic microtine cycles. In: Crisp, D. J. (Editor). *Grazing in Terrestrial and Marine Environments*. *British Ecological Society Symposium* 4: 57-68. Blackwell, Oxford.
- WATSON, A.; Moss, R. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. In: Watson, A. (Editor). *Animal Populations in Relation to their Food Resources*. pp. 167-220. Blackwell Scientific Publications, Oxford and Edinburgh.
- WATSON, J. S. 1961. Feral rabbit populations on Pacific Islands. *Pacific Science* 15: 591-3.
- WYNNE-EDWARDS, V. C. 1962. *Animal Dispersion in relation to Social Behaviour*. Oliver and Boyd, Edinburgh. 653 pp.