The lemming cycle

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Lemmings – and in particular the Norwegian lemming found in the Scandinavian Peninsula and Kola – are known for their extensive and fairly regular fluctuations in individual numbers.[1] There are folklore stories about these lemming cycles – as they are called. And there is a large body of literature on this phenomenon. Indeed, why lemmings (and other small northern rodents) exhibit such fairly regular cycles remains by and large an unsolved scientific problem – one of the classic problems in ecology.[2]

The modern scientific study of lemmings started with work carried out by the Norwegian Professor of Zoology Robert Collett, who at the end of the 19th century gathered a great deal of information about lemmings – and their variations in numbers. But it was not until the work of the British ecologist, Charles Elton, that the study of the lemming cycle saw its modern form. With the publication of Elton's paper[3] in 1924 the modern study of lemming cycles started.

To try to understand why lemmings fluctuate both regularly and extensively is indeed an important problem in ecology. Not only is such fluctuation found in several rodent species of the north. It is also found in other species, such as the Canadian snowshoe hare.[4] It is also of conceptually great value: as long as we do not understand the lemmings – and the other so-called cyclic species – we cannot claim that we understand population dynamics, the study of dynamics and regulation of populations.

The Norwegian Lemming – a key study animal in the field of population ecology. (Erika A. Leslie)

During the academic year 1996-97, an international team of scientists worked on this problem at the Centre.[5] The overall aim of our work was to analyse long-term data on lemmings and other periodically fluctuating species in order better to comprehend what the patterns to be explained are. Statisticians and ecologists worked together – and during the process developed new statistical models.

Among the discoveries during this period was the statistical documentation of phase-dependencies: during the increase phase of the population cycle, animals have a different dynamic structure than during the decrease phase. This had been a claim for many years – supported by experimental data – but never documented on the basis of statistical analysis of long-term population data. In a series of studies we demonstrated that such phase-dependency could indeed be found in natural systems.[6] This finding was a result of statisticians' favouring a particular form of non-linear models (the so-called threshold autoregressive models, essentially being piece-wise linear models[7]) and meeting up with ecologists working on the population cycles of northern mammalian species. Furthermore it was through long discussions – profoundly facilitated by the Centre-setting – that we were able to interpret biologically what the statistical results told us. These phase-dependencies could also be confirmed through our analysis of demographic data on survival and reproduction – primarily in a huge data set made available to us by Finnish colleagues.[8]

Another discovery – made after the period at the Centre, but conceived during the work at the Centre – is the importance of the length of the winter in the generation of the regular population cycles seen in lemmings and other northern rodents. This was understood by analysing data on the grey-sided vole in Hokkaido – a similar species to that found in Scandinavia. Again analysis of large amounts of time series data[9], made it possible for us to single out season as a key factor in the generation of the population cycle. As long as there is a so-called delayed density-dependence (which can be generated in a variety of ways, including through closed interactions between predators and the small rodents, as well as through closed interactions between small rodents and their vegetation), changing the length of the winter will change the population dynamics: in regions with short winters the populations may be stable (which indeed is observed), whereas in regions with long winters the dynamics may be lemming-cycle-like (again as observed). This is an interesting and important result, not least since scientists have been arguing – almost fighting – over the underlying reasons for the regular population cycles seen in lemmings and other small northern mammals. Our results suggest that it may not matter whether there is a closed interaction with the rodents involving predators or vegetation (over which scientists have been fighting) as long as one or the other link exists; what matters is the length of the winter (relative to the length of the summer).

Much further work is certainly required. However, we all feel that the work at the Centre provided the right platform and setting for generating these results. It is encouraging, though, that a detailed theoretical modelling study – also started during the period at the Centre – has confirmed the above predations.

So, can we say why there is a lemming cycle? Probably we can: it is most likely a result of a combination of either predation or interaction with its own food supply *combined* with the short summers (and long winters) in the regions where they live.

It is worth adding some more personal reflections on the importance of the Centre for Advanced Studies. My own experience is that it provides an ideal platform and atmosphere (involving hard work in the study chambers, relaxed and challenging discussions around the sofa table and short intensive workshops) for creative work. I for sure have benefited profoundly from my stay at the Centre – hopefully the scientific community may see some effects as well.

Notes:

[1] Stenseth, N.C. & Ims, R.A. (eds.). 1993. *The biology of lemmings.* Academic Press, London.

[2] Boonstra, R., Krebs, C.J. & Stenseth, N.C. 1998. Population cycles in small mammals: the problem of explaining the low phase. *Ecology* 79, 1479-1488.

[3] Elton, C.S. 1924. Periodic fluctuations in the number of animals: their causes and effects. *Journal of Experimental Biology* 2, 119-163. See also: STENSETH, N.C. 1995. The long-term study of voles, mice and lemmings: homage to Robert Collett. *Trends in Ecology and Evolution* 10, 512. Stenseth, N.C. 1999. Population cycles in voles and lemmings: density dependence and phase dependency in a stochastic world. *Oikos* 87, 427-460.

[4] Stenseth, N.C. 1995. Snowshoe hare populations: squeezed from below and above. *Science* 169, 1061-1062.

[5] Among the core members of this group was Nils Chr. Stenseth (Norway), Rudy Boonstra (Canada), Nigel Yoccoz (France and Norway), Charles J. Krebs (Canada), Howell Tong (Honk Kong and England) Kung-Sik Chan (US) and Takashi Saitoh (Japan).

[6] Framstad, E., Stenseth, N.C., Bjørnstad, O.N. & Falck, W. 1997. Limit cycles in Norwegian lemmings: tensions between phase-dependence and density-dependence. *Proceedings of the Royal Society of London, B* 264, 31-38. Stenseth, N.C., Chan, K.-S., Framstad, E. & Tong, H. 1998. Phase- and density dependency dynamics in lemming populations: statistical and mathematical modelling of periodic temporal fluctuations with a fixed periodic component sustained by environmental stochasticity. *Proceedings of the Royal Society of London, B* 265, 1957-1968. Stenseth, N.C., Falck, W., Chan, K.-S., Bjørnstad,, O.N., O'Donoghue, M., Tong, H., Boonstra, R., Boutin, S., Krebs, C.J. & Yoccoz, N.G. 1998. From ecological patterns to ecological processes: phase- and density-dependencies in the Canadian lynx cycle. *Proceedings of National Academy of Science, Washington* 95, 15430-15435. Stenseth, N.C. Chan, K.-S., Tong, H., Boonstra, R., Boutin, R., Krebs, C.J., Post, E., O'Donoghue, M., Yoccoz, N.G., Forchhammer, M.C. & Hurrell, J.W. 1999. Common dynamic structure of Canada lynx populations within three climatic regions. *Science* 285, 1071-1073.

[7] Stenseth, N.C., Chan, K.-S.1998. Non-linear sheep in a noisy world. *Nature* 394, 620-621. See also Yao, Q., Tong, H., Finkenstäd, B. & Stenseth, N.C. 2000. Common structure in panels of short ecological time series. *Proceedings of Royal Society of London, B*. 267, 2459-2467.

[8] Heikki Henttonen has been a long-lasting collaborator of us, although he was never proper part of the Centre. Prévot-Julliard, A.-C., Henttonen, H., Yoccoz, N.G. & Stenseth, N.C. 1999. Delayed maturation in female bank voles: optimal decision or social constraint? *Journal of Animal Ecology* 68, 684-697.

[9] Stenseth, N.C. & Saitoh, T. (eds.) 1998. The population ecology of the vole *Clethrionomys rufocanus*. *Researches on Population Ecology* 40, 1-158. Stenseth, N.C., Kittilsen, M.O., Hjermann, D., Viljugrein, H. & Saitoh, T. 2002. Interaction between seasonal density-dependence structures and length of the seasons explain the geographic structure of the dynamics of voles in Hokkaido: an example of seasonal forcing. *Proceedings of the Royal Society of London, B* (in press). See also Hansen, T., Stenseth, N.C. & Henttonen, H. 1999. Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density dependence. *American Naturalist* 154, 129-139.