Lemming cycles in captivity

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Summary. 2 freely growing confined populations of Norwegian lemmings displayed population peaks and declines which were similar to natural populations. In most other studies of confined populations of rodents, the number of animals stabilized and maintained fairly constant numbers. Juvenile mortality and reduced pregnancy rate contributed to the decline.

Many northern rodents display population cycles characterized by peak densities every 3-4 years. The Norwegian lemming, *Lemmus lemmus* (L.), is perhaps the most famous of these species. In addition to centuries-old accounts of this species, there are several fairly recent descriptions of fluctuating field populations of lemmings[1].

A laboratory stock of Norwegian lemmings has been successfully maintained during the past 12 years, thus enabling us to study in the laboratory the development of freely growing confined colonies of the Norwegian lemming. When such colonies were kept under constant environmental conditions with a surplus of food, we observed extreme changes in population density, similar to the peaks and crashes found in nature. This is quite surprising, since many studies of confined populations of other small rodents have revealed that after a period of growth, the population levelled off, often after some decline[2,3].

Our animals were kept in a pen 2×3 m, at temperatures of 15±2 °C, and light regime L/D=12/12[3]. The animals were supplied with rolled oats, bread, and apples ad libitum, and the floor was covered with hay and mosses, mostly *Pleurozium schreberi* which served as food, nesting material, and a substrate for the construction of runways. The food and litter were identical to that used in our breeding stock of *L. lemmus.*

The pen, in addition, was supplied with nestboxes (20×15×9 cm). The animals were banded or earmarked, and each week all animals were weighed and examined externally for health and breeding condition. Dead animals were removed from pens. Experiment 1 started with 1 male, 2 females and 4 nestboxes. The population had increased to 55 individuals by the 28th week, it then declined to 2 individuals before it again increased. Experiment 2 was initiated with 1 male, 3 females and 9 nestboxes. A peak of 115 individuals was reached in the 53rd week and was followed by a drastic decline to 7 animals in the 84th week when the experiment was terminated. The development of these 2 populations is shown in figure 1.

The fact that the 2 populations peaked at different densities is not surprising considering that the original animals

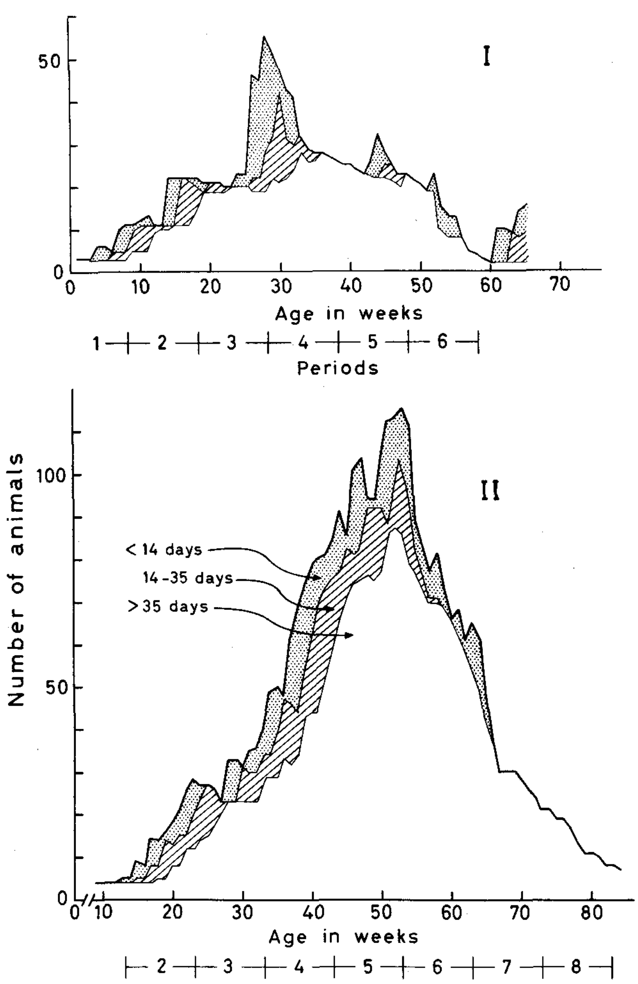

Fig. 1. Population development in 2 freely growing confined colonies of the Norwegian lemming.

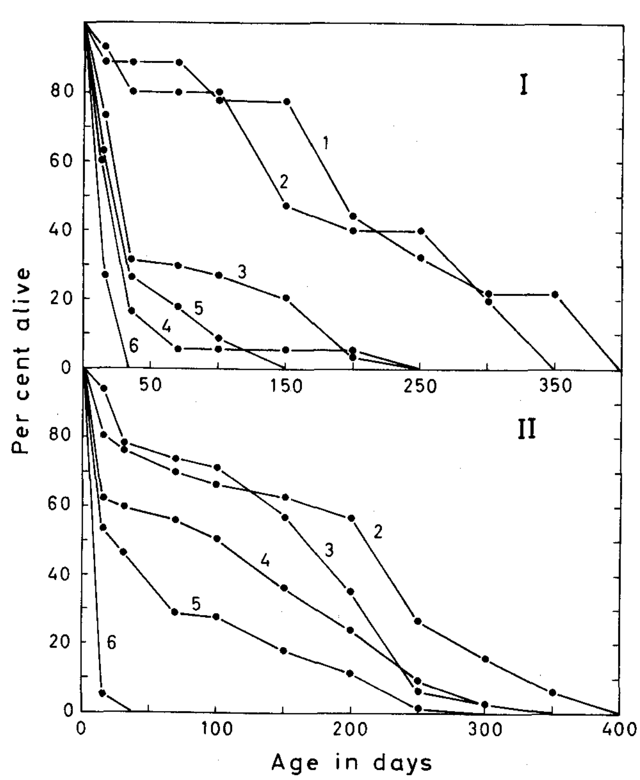

Fig. 2. Rate of survival of animals born in the colonies during different (1-6) population phases. (Refer to figure 1).

differed genetically, as did the number of nestboxes present. Large variations in peak densities of freely growing confined populations of small rodents raised under identical conditions have been observed earlier[3].

Confined populations of small mammals have been extensively used to study fundamental mechanisms of population regulation. The Norwegian lemming has been investigated by De Koch and Rohn[4], but the populations were provided with increased living area and were also disturbed by external factors and illness, making comparisons difficult. Clough[5] found that his confined populations of captive lemmings reached a near-steady level after 3–4 months, but his colonies were kept in smaller pens. The only case known to us where confined rodent populations behaved in a similar way to our lemming colonies is the population of nutria in the Philadelphia Zoological Gardens. The period was, in that case, 12 years[6].

In our experiments decline was caused by a combination of a reduction in the number of pregnant females and increased juvenile and adult mortality (figure 1). In fact, at comparable population densities, infant mortality was higher in the declining than in the increasing population, as evidenced by reduced life expectancy (figure 2). Animals born when the increasing population had 11–20 individuals in experiment 1, had an average life expectancy of 154 days compared to only 10 days for individuals born during the declining population phase. Increased density and eventual decline were characterized by an increase in the general activity, fighting, communal nesting and huddling. As in other studies, these changes in behavior were associated with severe juvenile mortality. Periods of increased infant mortality were associated with retarded growth, and the individuals which died shortly after weaning (i.e. between 2–3 weeks of age) showed signs of faltering already when 5–10 days old, when they were completely dependent upon the mother for milk and care. These effects may be caused by prenatal influences[7], maternal neglect and lactation failure[8], as well as the effects of huddling and overcrowding in the nest boxes[3]. Physiological changes, such as retarded growth, may persist in individuals for months after a population peak, a feature which has been shown in other rodents such as California voles[9] and in rabbits[10].

Part of the pen was occupied by more or less isolated, probably territorial, individuals, whereas the remainder was occupied by the subordinates. Huddling in nestboxes increased during the peak and decline phases and some nestboxes could house more than 20 adults. Hence, huddling had a detrimental effect on juvenile survival.

Our confined populations represent unnatural situations, especially since emigration of individuals was prevented. The results demonstrate, however, that even confined lemming populations, under controlled conditions, exhibit strong fluctuations in numbers. It was obvious that population parameters, such as infant mortality, are not simple functions of population density, but are dependent upon the population phase, i.e. whether increasing or declining.

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Potassium uptake by cold-resistant mouse L cells stored at low temperature

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Summary. Adaptation of a cultured mouse L cell population to 4 °C increased the survival of the cells and induced the uptake of potassium from the medium at this temperature.

Accumulation of intracellular potassium is known to occur not only in neurons, but also in other cell types before DNA synthesis and mitosis[1,2]. Intracellular accumulation of K^+ was also described in cold-stored cells and tissues of hibernators[3]. Previous experiments with cultured mouse s.c. fibroblasts (L cells) demonstrated an increased retention of K^+ in cold-stored sublines previously adapted to 4 °C, compared with that in unadapted parent populations[4]. Some findings even suggested the possibility of K^+ uptake in cold-stored, cold-adapted cells. To verify this possibility, we studied the changes in the intracellular K^+ concentration ($[K_i^+]$) in cold-stored LC3 cells, selected for cold resistance by repeated cooling of the parent L cell population[5]. The $[K_i^+]$ changes were estimated indirectly by measuring the K^+ concentration in the medium ($[K_e^+]$) of the closed culture system with ion-selective microelectrodes (ISMs) without disturbing the cells.

Materials and methods. A subline of the L cells called L-As and its cold-resistant derivative LC3[5] were stored for 4 weeks at 4 °C as fully grown monolayers of $2 \cdot 10^6$ cells in 5 ml of Eagle's minimal essential medium with 10% calf serum in Müller flasks. The number of living cells was estimated in 4 flasks of each population before cold exposure and then at weekly intervals by the dye exclusion test[5]. Simultaneously with cell counting, the K^+ content of their medium was measured in individual flasks with ISMs, prepared after Walker[6] in the modification of Vyskočil and Kříž[7]. The ISMs were first calibrated in a set of standard solutions of K^+, whose composition of Na^+ was as close as possible to that of the medium, and