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The oestrous cycle in the Norwegian lemming *Lemmus lemmus* (L.).

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In vaginal smears of Norwegian lemmings swelling of leucocytes was prevented by quickly drying the effluent using a hairdryer. The mean length of the oestrous cycle in captive lemmings was 5.6 days. About half of the animals rarely cycled and some spent the 2 weeks test-period in constant oestrus or dioestrus. It is suggested that the Norwegian lemming, like many microtines, is an induced ovulator, but that the system is flexible and modulated by social and other external stimuli.

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INTRODUCTION

The oestrous cycle gives important information about mammalian reproductive patterns. Vaginal smear histology has always been used as an index of the cyclical changes in ovarian activity and hormonal titers. In rodents such information is available not only from traditional laboratory animals such as the guinea-pig (e.g. Stockard & Papanicolaou 1917) the laboratory mouse (e.g. Allen 1922), and the rat (e.g. Long & Evans 1922), but also from several microtine rodents (see Hasler 1975). In the lemming tribe the oestrous cycle is described from the Brown lemming, *Lemmus trimucronatus* (Rich.) (Mullen 1968) and the Collared lemming, *Dicrostonyx groenlandicus* Traill, (Sayler 1969, Hasler et al. 1974), but it is not known for the Norwegian lemming.

By using a modification of the vaginal smear technique, it was possible to obtain vaginal smears from the Norwegian lemming. Based on this technique data are given about the oestrous cycle of captive Norwegian lemmings, and the results are discussed in relation to the reproductive strategy of this small rodent.

MATERIAL AND METHODS

Sexually virgine Norwegian lemmings from the laboratory stock at the Department of Biology, University of Oslo, were isolated at an age of 21 days and kept singly in steel cages. The light regime was 13 hours of full illumination and 9 hours of complete darkness, with one hour of halflight during the transitional phases. The temperature fluctuated between +10°C and + 14°C. The lemmings were kept and fed as described elsewhere (Semb-Johansson et al. 1991).

The vaginal lumen was flushed with an eyedropper filled with distilled water, 37°C. The effluent was spread on a glass slide and dried with a hairdryer in order to prevent the leucocytes from swelling. It was fixed for 5 min. in absolute alcohol, dried again and stained for 45 min. with Giemsa's stain.

Vaginal smears were taken from 20 animals every 12th hour during a 14 day period. The procedure was repeated during three different seasons, partly with the same animals. In all 40 animals were used, varying in age from less than 4 months to 2 years. Two animals, one of which showed a great number of leucocytes in the smears, were killed for histological examinations of the uterine and vaginal walls.

RESULTS

Only a few epithelial cells were found in the vaginal smears. Cornified cells were always present, sometimes in great numbers. The presence of leucocytes varied from a few to many. In individuals with distinct cyclic variations it was possible to record a phase where great numbers of cornified cells dominated the vaginal smears for about 2 days, and a phase where leucocytes dominated for about 1 1/2 days. Fig. 1 A shows the percentage distribution of cornified cells, leucocytes and epithelial cells in the smears during a fortnight period in an animal which cycled

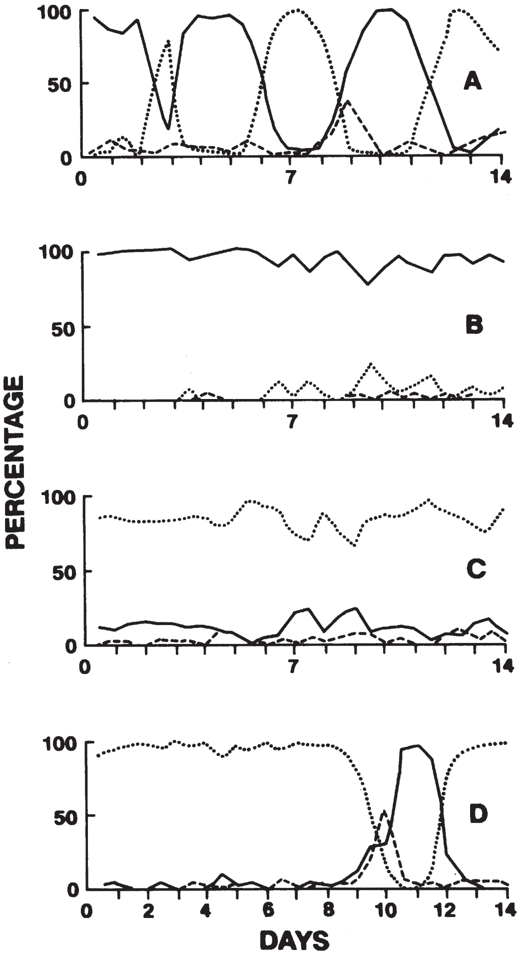

Fig. 1. The percentage distribution of different cell types in vaginal smears from the Norwegian lemming. The figures show females with regular oestrous cycles (A), constant oestrus (B) and dioestrus (C), interrupted by one single cycle (D). ——: cornified cells; - - - -: epithelial cells; . . . . .: leucocytes.

Table 1. The frequency distribution of length of cycles.

Length of cycles in days	4	4.5	5	5.5	6	6.5	7	7.5	8	8.5	9
Number of cycles	3	1	10	3	7	1	0	1	0	1	1

N: 28; $\bar{x}$: 5.6±1.2

regularly. While both cornified cells and leucocytes periodically made up nearly 100% of all cells, the percentage of epithelial cells was usually below 10 and did not show any cyclic variation.

The sudden abundance of cornified cells compared with leucocytes in the vaginal smear marks the beginning of the oestrous phase (Allen 1922, Long & Evans 1922). The length of the oestrous cycle is in the present paper taken as the difference in days between the first days of two successive oestruses. The frequency distribution of the length of the cycles is shown in Table 1. The mean value was 5.6±1.2 days, the mode 5 days.

The 40 experimental animals could be classified as follows:

1. 21 individuals showed regular oestrous cycles (Fig. 1 A). Three of these animals were tested at two different seasons.

2. 19 individuals exhibited different types of irregular patterns. All except 6 of these animals were tested at two different seasons. The 19 animals could be grouped as follows: a) 7 animals had closed vagina, b) 3 animals showed mostly cornified cells in the vaginal smears during the whole test period and were considered to be in constant oestrus (Fig. 1 B), c) 2 animals showed mostly leucocytes in the smears during the test period and were considered to be in dioestrus (Fig. 1 C). d) The rest (7) was animals with a combination of the above-mentioned types (Fig. 1 D).

Microscopic sections of the vaginal wall from an animal where the smear revealed abundance of cornified cells, showed a layer of cornified cells facing the lumen. They covered a layer of epithelial cells of variable thickness. Some of the cells seemed to be in a state of transformation from epithelial cells to cornified cells. Some leucocytes could be seen among the epithelial cells. Sections of the uterus showed a layer of epithelial cells facing the lumen with some dispersed leucocytes in between. The most striking feature in the microscopic sections from the uterus was the marked vascularity.

In microscopic sections of the vagina from one individual with predominance of leucocytes in the vaginal smears, the epithelium facing the lumen appeared single-layered. Leucocytes were present near this layer. Sections from the uterus showed leucocytes in quantities facing the lumen. The epithelial layer was thicker. There was no vascularity in the uterine walls.

DISCUSSION

Based on the relative abundance of cell types the oestrous cycle in the guinea-pig, laboratory mouse and rat is normally divided into 5 different phases. In the pro-oestrous phase nucleated epithelial cells dominate. In the Norwegian lemming nucleated epithelial cells never occurred alone or dominated the smears. This indicates that there are species differences in the cellular composition of the phases of the oestrous cycle, although the normally short duration of the pro-oestrous phase makes it difficult to detect this phase.

The length of the oestrous cycle of the Norwegian lemming (mean 5.6, mode 5 days) is typical for many small rodents, e. g. *Microtus* spp. such as *M. montanus* (Peale) (5 days; Gray et al. 1974), the Chinese hamster, *Cricetulus griseus* Milne-Edwards (4.3 days; Parkes 1931), and the Steppe lemming, *Lagurus lagurus* (Pallas), (5 days; Kretschmer & Freye 1977). In the Collared lemming the cycle was found to be about 10 days (Sayler 1969).

In the present study irregularities in the oestrous cycle were found among all age groups and at all seasons. A high proportion of the animals showed no cyclicity at all. This seems to be the case in many species: a certain number of females rarely cycles and spends prolonged periods in different stages of the oestrous cycle. Thus in the Collared lemming about 1/3 of the animals never cycled (Sayler 1969). In the Steppe lemming Whitney and Burdich (1966) found a vaginal cycle in only 2 out of 20 females, whereas in the Brown lemming non-pregnant females remained in constant oestrus during the summer and constant di-oestrus during winter (Mullen 1968).

The present set of data does not allow for any safe conclusion about the type of ovulation in the Norwegian lemming. One interpretation is that this species remains in constant prolonged oestrus (Fig. 1 B) or di-oestrus (Fig. 1 C), and that ovulation is induced. This is suggested for the Brown lemming (Mullen 1968) and is known to occur in the Collared lemming (Hasler & Banks 1973) and in several *Microtus* species. It is considered characteristic of short-life span, highly productive prey species (Connaway 1971), and it would benefit the recovery from low population density. Zarrow & Clark (1968) suggest that the presence of penile spines may indicate reflex ovulation. Penile spines are present in the Norwegian lemming (pers. obs.). If the Norwegian lemming is an induced (reflex) ovulator, Fig. 1 A could be explained by ovulation being induced by cervical stimulation from the pipette, although more or less well-defined periods of oestrus do occur in females of many reflex ovulators (Milligan 1982). An other explanation is that the cycles are the results of spontaneous ovulation, an ovulation strategy favoured by relatively social species (MacFarlane & Taylor 1982).

The type of oestrous cycling found in a species is probably not a priori a systematic characteristic, but is adjusted to the biology of the species in such a way that it maximizes the fitness of the individual. As part of this strategy, the oestrous cycle and the type of ovulation may be modifiable by external influences, the population phase and the social position of the individual. It is in this connection interesting to note that the rat possesses both pathways for producing the high LS surge necessary for ovulation (Brown-Grant 1975). In the Wood mouse, *Apodemus sylvaticus* (L.), only about 15 per cent of the females had oestrous cycles and spontaneous ovulation. The rest did not ovulate spontaneously; the differences were apparently determined genetically (Clarke 1985). In the House mouse a population may consist of types of individuals with different oestrous cycle reactions to external influences (Massey 1986).

In the Norwegian lemming induced ovulation would be the optimal solution during a population low, whereas spontaneous ovulation would function well during the peak period. The great individual variation found in the oestrous cycle in the present study may therefore be a reflection of the flexibility of the cycles and of the type of ovulation in the Norwegian lemming.

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