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Population Dynamics and Individual Features during the Phase of Decline in the Field Vole

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A North Swedish population of the field vole *Microtus agrestis* (Linnaeus, 1761) in the phase of decline was studied in detail by the use of individual marking and brief trapping intervals over one reproductive season. In early spring, a distinct surplus of males was found. Reproduction started with a delay of about 4 weeks, thus the first juveniles could not be trapped earlier than the beginning of June. All the overwintered adults disappeared during 10 days just prior to the recruitment of the young, resulting in a total exchange of the population. The members of the spring born cohort ceased growing at an age of about 25 days and maintained body weights of 20—30 g during the entire time of observation. Although sexual activity was obvious in both sexes, no juveniles could be trapped during summer. Both immigration and emigration was scarcely seen. Thus during summer, the population remained rather uniform with respect to number, age and weight, closely resembling a pattern found during winter. The reasons and implications of these findings are discussed.

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1. INTRODUCTION

Microtine cycles have been well known for a long time (Howell, 1923; Elton, 1924) and have been focussed on by many population biologists. Therefore, extensive knowledge of geographical distribution (*e.g.* Myllymäki, 1977 b) and of typical cycle characteristics (*e.g.* Krebs & Myers, 1974) is available today. However, both the driving mechanisms behind these cycles and, as a consequence, the ecological implications inherent in this strange manner of regulating population density, are still under discussion.

The phase of decline is of particular interest, because changes in population parameters occur quite rapidly. It has been the subject of many investigations, but in most cases comparisons have only been able to consider population structure before and after the decline. So Myllymäki (1977a) deplores the lack of more detailed data especially for this phase, which he argues is caused by "practical difficulties in obtaining adequate material". For the most part this is an inevitable problem when investigating under low density conditions, because there are only a few individuals available. Thus quantitative results must be based on small numbers, and statistics remain uncertain.

We tried to overcome this problem by conducting a permanent and detailed survey of a free-living population of *Microtus agrestis* (Linnaeus, 1761). Intensive live-trapping at regular, brief intervals and the resultant knowledge of all individuals living in the trap area allowed a very close observation of the population. Our special interest centered on the features of individuals and correlated changes in the population structure.

2. MATERIAL AND METHODS

The investigation was carried out in the North Swedish province of Västerbotten from the 11th May to the 10th September, 1982. The research area is situated 30 km south of Umeå near the Bottensea (63°35′ N, 19°50′ E). It encloses some abandoned pasture land in which *Alopecurus pratensis* and *Deschampsia caespitosa* are the dominant graminaes. This type of biotope offers optimal conditions for the field vole and is widely spread over Västerbotten which causes the frequency of high densites and severe damage in this part of Sweden (Larsson, 1975; Myllymäki, 1977 b; Hörnfeldt, 1982).

The development of the population was examined by the CMR-method. 48 live-traps ("Oos-Drahtgitterfalle") were arranged in a grid covering an area of 30×40 m, the grid width was 5 m. The trap area was surrounded by a coniferous grove, a small brook, an unsurfaced road and dry ditches so that it could almost be considered as secluded. Captured voles were marked individually by toe-clipping and at every catch trap position, time of control, weight and state of reproduction were noted.

Each month was divided into three 10 days-periods ("decades") with trapping times on the 3rd, 6th and 9th day, resulting in a total of 36 trapping days. During these days, traps were checked in 4-hour intervals over a period of 24 hours, so that the data is based on 216 trap controls altogether. Between the trapping days, traps remained in the grid freely approachable and baited, but not set up for catching.

During the peak phase of the cycle in summer 1981 (Hörnfeldt, 1982) a population was analyzed (July/August) by similar methods on a trap grid of 3000 m² in the vicinity. Some results of this investigation are presented for comparison.

3. RESULTS

3.1. Density and Reproduction

During the entire period of investigation a total of 50 individuals was captured (32 males and 18 females). The number of individuals in the grid ranged from 19 to 9 per decade. (During the following peak phase in summer 1984 a maximum of about 80 individuals was estimated on the same meadow (Brenner, in prep.)). Out of the 50 individuals, 15 animals were captured during one 10 days-period only (8 of them only once); 35 individual were thus resident for more than one decade. Their recruitment, time of residence and state of reproduction can be seen in Fig. 1, and the development of weight in Fig. 2. From this data several features of the population can be described.

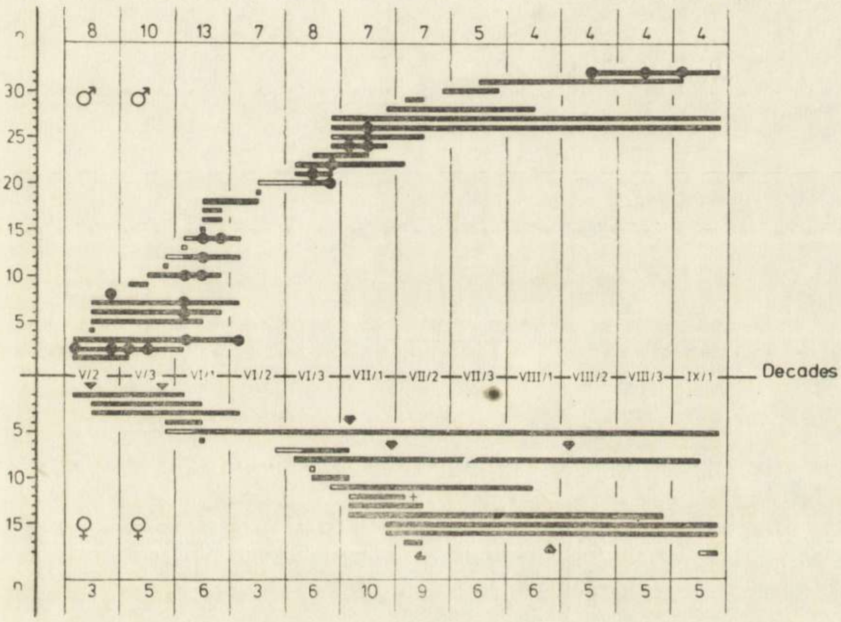

Fig. 1. Development of the population during the period of investigation May—September 1982. Each bar represents one individual. — n: ordinate=total of males and females, absissa=number of males and females during one decade. — Squares: individuals observed during one decade only. — Open bars: period of juvenile state (body weight not above 15 g). — Dots: males found with scrotal testes. — Arrows: weight diminution indicated birth. — Cross: vole found dead in trap.

1. The maximum number of 19 individuals was found during decade VI/1. After a temporal low of 10 individuals during decade VI/2, the number rose up again to 17 individuals during decade VII/1. Thereafter, a continuous diminution reduced the total to 9 individuals.
2. The population during early spring was represented by heavy adult individuals which had obviously overwintered. There was a distinct surplus of males (about 70%) and most of them were sexually active.
3. Between the 6th and the 16th June, all these individuals suddenly disappeared. Subsequently, only previously unknown voles were found

in the grid (one female emerged during decade V/3). The vast majority of them were significantly smaller (*c.f.* 3.2.), which indicated that they belonged to a newborn generation. Thus, there was a nearly complete exchange of the population living in the grid, obviously caused by the change of two different generations.

4. Within the new generation, the sex ratio was nearly balanced. Sexual activity was observed in most of the males up to the middle of July. After this time only one male with scrotal testes was found resident.

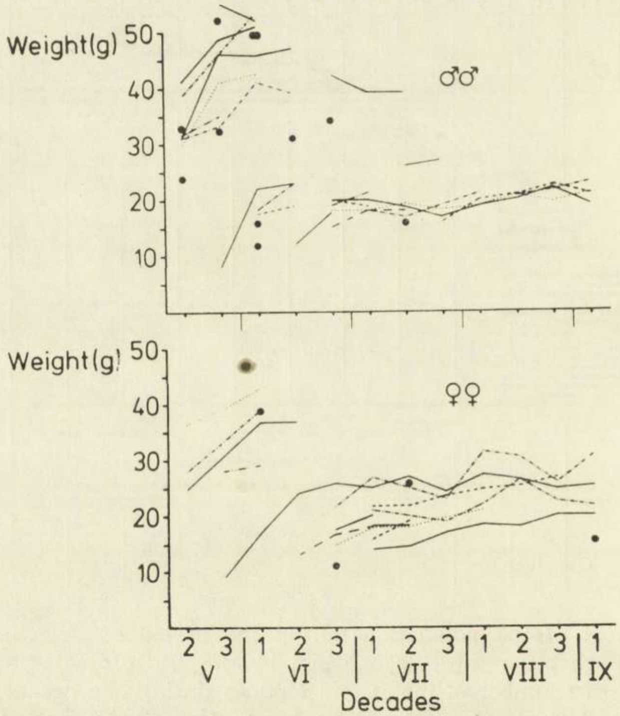

Fig. 2. Development of individual body weights of males and females. Each value is the average of weight during one decade. — Dots: weight of individuals observed during one decade only.

Pregnancy was found in four individuals of the spring born cohort (31% of the females). One female had two pregnancies within five decades while the others were pregnant only once. The time of birth was indicated by abrupt changes in body weight. The calculated period of gestation was about 20 days which is normal for *M. agrestis* (Krapp & Niethammer, 1982). Nevertheless, recruitment of young was negligible. Only one further juvenile could be trapped during decade IX/1.

5. From decade VI/2 onwards, only 4 animals could be followed for no longer than one decade (one further animals was found just before the

end of the programme which was the reason for its short registration). On the other hand, 7 individuals could be followed for more than two months in the unfenced grid. Both findings indicate that there was only slight immigration into the grid from surrounding areas as well as emigration out of the grid.

3.2. Body Weight

In Fig. 2, the "population sections" before and after decade VI/2 are clearly separated by the course of weight development. The overwintered cohort consisted of heavy individuals of 30—40 g which showed a distinct increase of weight during May and the beginning of June. The members of the spring-born cohort were first trapped with weights of about 15 g, which classifies them as juveniles. Only a slight increase could be observed during the following weeks to give a final body weight of 20—30 g, which was then maintained during the whole summer.

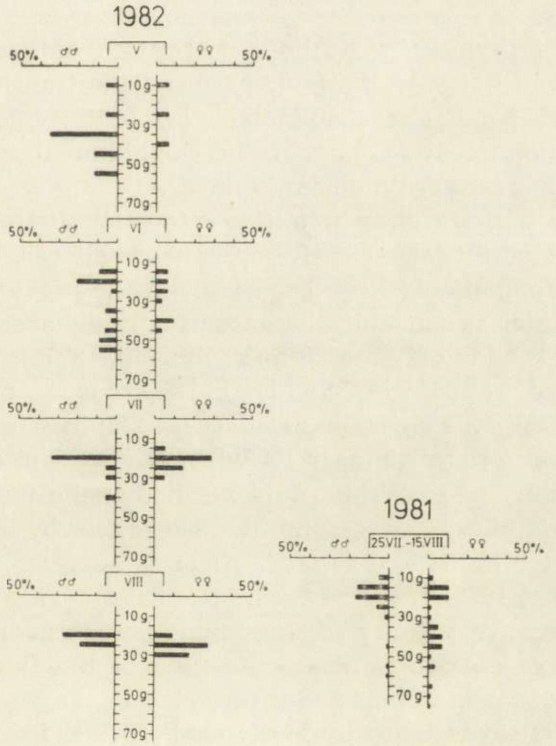

Fig. 3. Population structure during the decline phase 1982 for each month May—August and the peak phase 1981 (25.VII.—15.VIII.). Each bar represents the percentage of one weight-class (5 g) within the population (=100%).

The early cessation of growth as well as the lack of juveniles during summer resulted in a drastic change of the population structure (Fig. 3). In August, extreme weight-classes were no longer present and the whole population was confined to three 5 g-classes only. In summer 1981 juveniles of both sexes, which are represented by the two lowest classes, were present in large numbers and the weight-classes of more than 30 g were well represented.

4. DISCUSSION

In 1982 a general diminution in the numbers of *M. agrestis* was found in the whole province of Västerbotten (Hörnfeldt, 1982). So it is quite obvious that the population under study passed through a cycle dependent decline. Following the classification given by Chitty (*c.f.* Krebs & Myers, 1974) the temporal course of decline was of type G, in which the decrease starts during winter and continues until the following summer. This type of decline seems to be the most common pattern for *M. agrestis.*

Therefore, it is evident that the investigation did not concern the decline as a whole but only the later part and the transition to the low phase, when the population maintains a low density level. The most important question for this part of the population cycle is why the density did not increase again during summer.

The field-data already gave prominence to early June when the population was devided into two clearly separated "sections". The individuals of the earlier group should have been born in the previous autumn and have entered winter as subadults, because usually the overwinter survival rates of the last cohorts only are high (Myllymäki, 1977a).

An unexpected result was the distinct surplus of males which is rather unusual in *M. agrestis* populations. Myllymäki (1977 a) for example describes a sex ratio near 1:1 when the overwintered population enters the breeding season. This could mean that the population was in a "state of instability", an assumption suggested by experiments of Redfield *et al.* (1978) with the North American species *Microtus townsendii* (Bachmann, 1839). The low ratio of females during spring resulted in a low reproductive potency of the population. In addition the beginning of June was considered to be the time of the first litters which means a delay of about 4 weeks. Such a delay in the year of population decline has also been reported by Myllymäki (1977 a) from Finland. Both the belated start of reproduction and the small ratio of females lead to the expectation of a numerically small spring born cohort.

At the beginning of June, the whole overwintered cohort disappeared from the grid within 10 days. It appears that just after weaning the adults died or possibly emigrated (Halle, 1984), whereas their young remained stationary. The spring-born cohort was a very homogeneous group because all members descended from one litter period and the course of individual development was quite similar. Their most characteristic feature was an early cessation of growth at ages of about 25 days. Compared with data given by Myllymäki (1977 a) for the peak phase, the spring-borns of the declining population reached only half the weight of individuals from the same seasonal generation after 60 days.

The fact that voles of the peak phase are much heavier than those after the decline is well known and has already been pointed out by Chitty (1952), Zimmermann (1955) and Chitty & Chitty (1962). The results presented here suggest a possible explanation for this finding. Voles born in late summer and autumn normally cease growing at about 25 g and they winter as subadults (Reichstein, 1964; Myllymäki, 1977 a). Furthermore, the population structure described by Hansson (1971) for a South Swedish population in December was very similar to the one we observed in August, with the whole population being spread over only three 5 g-classes. It seems that during the decline phase the same process which occurs at the beginning of winter affects the voles born during the most productive time of the year, thus causing growth to cease at about 25 g.

Despite the striking similarities in weight development, the small individuals during decline can not really be classified as subadults, because some of them were found to be breeding. Sudden weight diminution of pregnant females made certain that litters were forthcoming and easily perceptible nipples indicated attendant lactation. Nevertheless, no juveniles could be trapped during July and August. Thus an extremely high juvenile mortality must be assumed for the early postnatal phase, which was also found by Chitty (1952) and Godfrey (1955) for *M. agrestis* during the decline.

The causes for this curious situation remain uncertain. Both severe external and internal influences were not obvious, so it seems reasonable to look for more subtle environmental conditions especially connected to the low phase. As indicated in Fig. 2, immigration of strange adult voles into the grid occured only exceptionally after the population exchange, so that the population was composed nearly exclusively of litter mates during summer. This situation was simulated by Batzli *et al.* (1977) with caged North American species. They concluded: "If young voles remain close together in the field, one might expect lower growth and reproductive rates." The mechanisms responsible seem to be based on physical and olfactory contacts between the litter mates. In *M. agrestis* similar effects were found by Wilson (1973) and Clarke (1977). Several features of the population observed resemble these experimental findings closely, suggesting causal relationship between the peculiarities of growth and reproduction and social conditions during a population low.

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DYNAMIKA POPULACJI I CECHY OSOBNIKÓW W FAZIE SPADKU LICZEBNOŚCI NORNIKA BUREGO

Streszczenie

Badano fazę spadku w cyklu populacyjnym *Microtus agrestis* w Północnej Szwecji. Norniki łowiono w krótkich odstępach czasu w ciągu jednego sezonu rozrodczego i znakowano indywidualnie. Wczesną wiosną w populacji znacznie przeważały samce (Ryc. 1). Młode pojawiły się dopiero na początku czerwca, co było skutkiem opóźnienia rozrodu o około cztery tygodnie. Wszystkie przezimki zginęły w ciągu 10 dni tuż przed wyjściem młodych, co spowodowało całkowitą wymianę osobników w populacji. Wszystkie zwierzęta urodzone wiosną (kohorta wiosenna) zakończyły wzrost w wieku około 25 dni i utrzymywały ciężar ciała na poziomie 20—30 g przez cały okres badań (Ryc. 2). Chociaż samce i samice były aktywne płciowo, w ciągu całego lata nie schwytano ani jednego młodego osobnika. Rzadko notowano przypadki migracji. W rezultacie od zimy do początku lata struktura populacji była podobna pod względem liczebności, wieku i wagi osobników. Dyskutowane są przyczyny i implikacje wykrytych zjawisk.

BOOK RECEIVED

Thomas H. Kunz, (ed.) 1982. Ecology of Bats. Plenum Press. New York and London. 1—425. [With 69 Figs. & 25 Tables]. Price 49.50 US dol.

Liczba prac z zakresu ekologii nietoperzy w ostatnich 20 latach rośnie lawinowo i trzeba już było dokonać jakiejś syntezy. W dotychczasowych monografiach poświęconych nietoperzom ekologia była traktowana jako jeden z rozdziałów, choć współcześnie rozwija się bardzo żywo, zwłaszcza w Ameryce.

"Ecology of Bats" — dzieło pod redakcją jednego z najwybitniejszych na świecie ekologów nietoperzy Thomasa H. Kunza jest syntezą stanu wiedzy z tej dziedziny. T. H. Kunz zdołał zebrać do swojego dzieła doborową i najbardziej liczącą się obecnie na świecie stawkę chiropterologów, zajmujących się ekologią tych stale jeszcze mało poznanych ssaków.