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**Age Structure and Dynamics of Numbers in
an Island Population of Bank Voles**

[With 1 Table & 5 Figs.]

Using material obtained over a four-year period from trapping an island population of *Clethrionomys glareolus* (Schreber, 1780) in live traps, and also several studies dealing with these materials, an examination was made of the changes in the age structure of the population over the yearly cycle and also over a period of several years. Variations in age structure in relation to data on natality, capacity for survival and dynamics of numbers indicate that there is a 2-year cycle in the study population. A description is given of the pattern which this cycle is assumed to follow.

1. INTRODUCTION

The age structure of rodent populations, including that of *Clethrionomys glareolus* (Schreber, 1780), has been the subject of a number of detailed studies (*inter alia* Zejda, 1961; Ilyenko & Zubčaninova, 1963; Bergstedt, 1965; Kubik, 1965). However, these authors concentrated on general changes in age structure over the yearly cycle, mostly to trace from it processes of natality and mortality taking place in the populations, processes which are more difficult to record directly.

The present study is based on detailed material obtained during the course of long-term team investigation of an isolated island population of *C. glareolus*. Many of the studies describing the different processes taking place in this population have been published earlier. The author, having at her disposal material from years with different dynamics of numbers and also numerous works, has attempted to connect age structure with dynamics of population numbers. The purpose of the study was to ascertain whether age structure is, at some given moment in the

life of the population, a factor shaping population numbers and their dynamics.

The relations described here apply only to one definite isolated population of bank voles. The connections between a population's age structure and its number are undoubtedly different in populations of this species not limited by sharply defined habitat boundaries, that is, population in which the individuals are able freely to interchange and disperse, and also in populations of different species.

2. STUDY AREA AND METHODS

Studies were made of an isolated population of *C. glareolus* inhabiting an island. The material used in the present study was obtained mainly from 1966—1969, and partly from 1970. The 4-hectare island situated in Lake Bełdany (northern Poland) is covered by forest composed of the following three phytosociological associations: *Salici-Franguletum* Malc., 1929; *Circeo-Alnetum* Oberdorfer, 1953; *Tilio-Carpinetum* Traczyk, 1962. A detailed description of the habitat is given by Traczyk (1965) and Andrzejewski, Petruszewicz & Waszkiewicz-Gliwicz (1967). Captures were made in live traps set on 159 sites distributed evenly over the whole island. The animals were marked individually by toe-clipping. Every year 5 two-week series of captures were made from mid-April to the end of October covering the whole reproduction season. Details of methods are to be found in the study by Gliwicz *et al.* (1968).

The studies provided detailed information on the fate of individuals belonging to four cohorts, *i.e.*, groups of individuals of similar age born at different times during the reproduction season. The fate of these individuals was traced from the time of their first capture (which may take place about the 21st day of life, but on an average occurs at the age of 6 weeks) until the last trapping period before their disappearance from the population. Data on the average day of birth of the whole cohort and numbers in this cohort at the time of birth were calculated on the basis of dynamics of numbers of pregnant females (Bujalska *et al.*, 1968; Bujalska, 1970).

In effect the following lived in the population each year: individuals belonging to the early-spring cohort K_1 , average date of birth beginning of May, recorded in traps for the first time between 1—15 June; individuals from the spring-summer cohort K_2 , average date of birth mid-June, caught for the first time in the second half of July; individuals from the summer-autumn cohort K_3 , average date of birth about 30 July, which began to be caught between 1—15 September, and finally individuals from the autumn cohort K_4 , born about 15th Sept., recorded for the first and only time during the year of birth in the trappable¹ part of the population in the second half of October.

In addition there is also a certain group of the previous year's overwintered individuals originating from all four cohorts of the previous year, and given the joint name of »cohort« K_0 . In April, at the beginning of the reproduction season, these individuals formed 100% of the population, but with the passage of time, due to their disappearance from the population and entry into it of young individuals, the role of overwintered individuals gradually decreases.

¹ Individuals are included in the trappable part of the population from the time of their first capture.

3. VARIATIONS IN POPULATION INDEXES OVER A LONG-TERM CYCLE

It is known from earlier studies that some population indexes remain unchanged in the study population from year to year (Petrušewicz *et al.*, 1971). Among these is the number of individuals born in a population during each reproduction season (Bujalska, 1970). During the years referred to, *i.e.*, 1966—1969² these numbers were as follows: in 1966 — 1048, in 1967 — 1089, in 1968 — 1011 in 1969 — 1050 newborn voles. The next very stable value is the number of individuals surviving the winter and forming the »basic stock« of the population the following year. During the study years these numbers were: 1966 — 56 overwintered individuals, 1967 — 68, 1968 — 70 and 1969 — 62 individuals. This

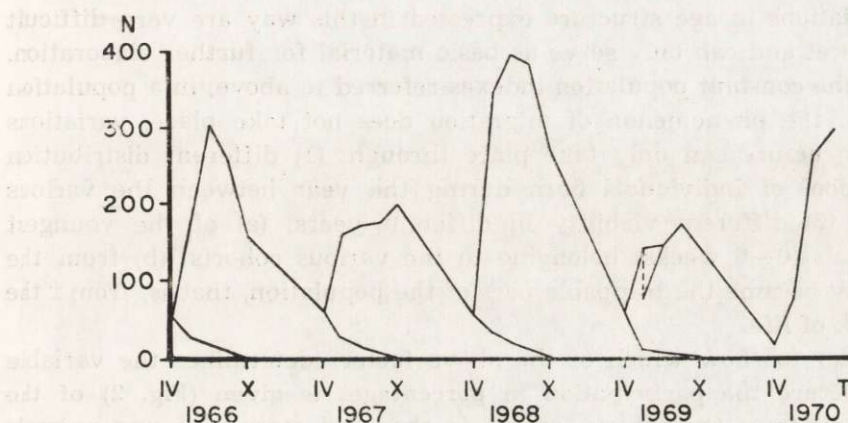


Fig. 1. Dynamics of population numbers.

means that the combined mortality of all individuals in a population over the whole year is uniform in each of the study years and that the same number of individuals »pass« through the population.

On the other hand there is considerable variation in the dynamics of population numbers over a long-term cycle (Fig. 1). At the peak there were 399 individuals in the population in one year and only 176 in another. The time at which the peak occurred in the population also differed; in years when numbers were high this peak usually

² Studies on the island population have now lasted 9 years, but only material from the first 3 years (1966—1968) made it possible to trace the natural life cycle of the population, as attempts were made at controlling the development of the population in subsequent years. Material from 1969 is thus not completely »pure«, as 40% of the individuals from the spring cohort were removed from the population that year. According to Bujalska (1973), however, the population very soon compensated for this loss and therefore it was decided to include these data in the present study, though bearing their specific nature in mind.

occurred early in the reproduction season, i.e., in July, while in years with low numbers, not until September.

4. AGE STRUCTURE

The age structure of the study population can also be considered as among variable indexes. The cohort was taken as a unit of age structure here, and variations in age structure were traced over a long-term cycle, also taking into consideration the percentage formed in the population by newborn individuals not caught in traps in the given trapping series. As their numbers were estimated in a way different from the numbers of the trappable part of the population and refer to the whole period of 0—6 weeks, they cannot be directly compared. The variations in age structure expressed in this way are very difficult to interpret and can only serve as basic material for further elaboration.

With the constant population indexes referred to above, in a population in which the phenomenon of migration does not take place, variations in age structure can only take place through: (1) different distribution of the pool of individuals born during the year between the various cohorts; (2) different viability in different years: (a) of the youngest individuals (0—6 weeks) belonging to the various cohorts; (b) from the time they became the trappable part of the population, that is, from \pm the 6th week of life.

In order to show which of the above factors determines the variable age structure the participation in percentages is given (Fig. 2) of the individuals from the various cohort in the total mass of young animals born in a given year (column 1) and the percentage of these individuals in the group surviving to trappable age (column 2). The first two columns from each year do not thus illustrate the true age structure of the population at any given definite moment of time, but only the structure of groups of uniform age from which individuals enter the population at different moments. The cohort proved to be too small a unit and changing in too random a fashion from year to year to permit of grasping any regularity in variations over a long-term cycle. Therefore the fates of the first two cohorts K_1+K_2 (spring generation) and the two later cohorts K_3+K_4 (autumn generation) were compared with each other.

During the study years, irrespective of the picture of variations in numbers, the numbers of individuals born during the first half of the reproduction season (K_1+K_2) are slightly higher than the number born during the second half of the season (K_3+K_4) and exhibit a more or less stable ration in relation to each other, as follows: 56 : 44 in 1966, 55 : 45

in 1967, 53 : 47 in 1969 and exceptionally 69 : 31 in 1968. Thus in accordance with the assumption put forward by Bujalska (1975), it is not the different distribution in time of young born, but their viability which is responsible for the differing picture of dynamics of numbers in different years. Although the average viability of individuals of all cohorts from birth to about the 6th week of life was similar in 1966, 1967 and 1969, respectively 34.8%, 31.6% and 34.1% and was generally greater in 1968 (50.3%). But, as Bujalska (1975) showed for the same population, in years with high average numbers the average length of life of individuals belonging to the spring cohorts is far longer than it is for individuals belonging to the autumn generation, while in years

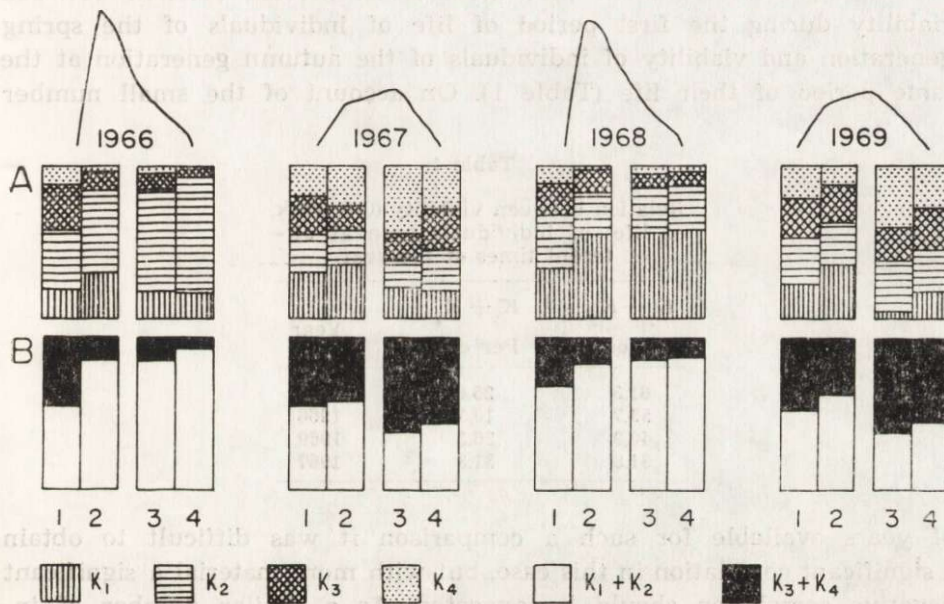


Fig. 2. Percentage formed by the various cohorts at different periods in the life of individuals (column 1 and 2) and the population (column 3 and 4). Columns: 1 — Individuals born in a given year (0 weeks of age), 2 — Individuals entering the population (6 weeks of age), 3 — Population at the end of the reproductive season, 4 — Population at the beginning of the following reproductive season.

with low average numbers the two values are almost identical. She also found a significant positive correlation between viability of individuals from the spring cohort during the first period of life (0—6 weeks) and average population numbers.

It can be seen from column 2a and b in Fig. 2 that there is a marked difference between the percentage composition of individuals from dif-

ferent cohorts at the time they entered the population (became trappable) and thus in reality between their viability from birth to this time. In years of high dynamics of number, that is, in 1966 and 1968, individuals from the autumn generation (K_3+K_4) had a far lower capacity for survival than individuals from the spring generation (K_1+K_2) and consequently the percentage of numbers $N(K_1+K_2) : N(K_3+K_4)$ at the moment of entry into the trappable part of the population appears as 87 : 12 in 1966 and 85 : 15 in 1968. In years with a flatter curve of dynamics of numbers, that is 1967 and 1969, the viability of cohorts during the first period of their life is more or less uniform and the percentage of numbers $N(K_1+K_2) : N(K_3+K_4)$ was respectively 56 : 44 and 63 : 37.

It would therefore seem that there is an inverse relation between viability during the first period of life of individuals of the spring generation and viability of individuals of the autumn generation at the same period of their life (Table 1). On account of the small number

Table 1

Relation between viability (0-6 week of life) of individuals born at different times of the year.

K_1+K_2	K_3+K_4	Year
Per cent	Per cent	
61.3	25.0	1968
53.7	10.3	1966
40.9	26.5	1969
31.8	31.3	1967

of years available for such a comparison it was difficult to obtain a significant correlation in this case, but with more material a significant negative correlation should be expected. As a similar number of individuals is born from year to year in the cohorts, and the mortality of later cohorts appears to depend on the mortality of the earlier cohorts, this last parameter appears to have an undoubtedly important effect on the course of the age structure and dynamics of population numbers in a given year.

Bujalska (1975) found that the viability of young animals during the period from birth to the 6th week of life is positively correlated with the viability of the mothers of these individuals. In the light of what has been said above, this relation would appear particularly important for the younger individuals from the spring generation and their mothers which — in the case of K_1 solely, and in the case of K_2 in the great majority — originate from the group K_0 (overwintered animals). Ex-

amination was therefore made of the age structure and capacity for survival of these overwintered individuals.

The age composition of the cohort K_0 depends in the following year on the age structure of the population in a given year, which means on (1) numbers in the various cohorts at the time of their entry into the trappable part of the population; (2) their mortality from this time up to the end of the reproduction season and (3) on their mortality during the winter. The viability of trappable individuals in the given reproduction season depends on their age (Petrusewicz *et al.*,

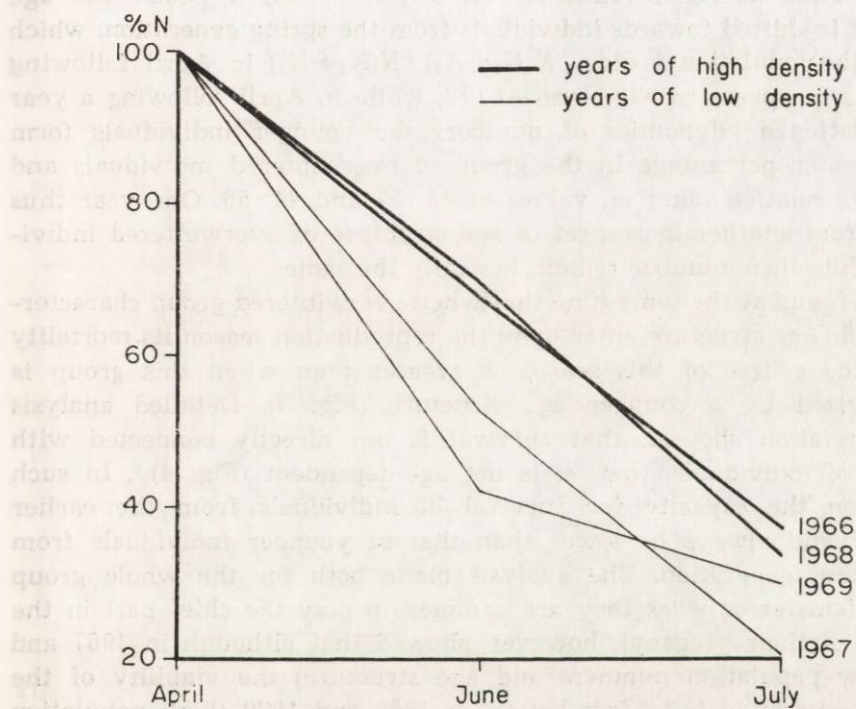


Fig. 3. Survival of overwintered animals (K_3).

1971). Individuals from cohort K_1 have the greatest capacity for survival (calculated for one day) and those from cohort K_4 the least capacity. The period from the moment of entry into the population up to the end of the reproduction season, however, lasts longer for the earlier cohorts and shorter for later cohorts. Cohort K_1 and K_2 have a relatively low mortality but is affected by mortality for longer time than cohort K_3 or K_4 , which are characterized by higher mortality. As the result of these two elements overlapping, the population's age structure at the end

of reproduction season, that is at the end of October (Fig. 2 column 3 a and b), is similar to the structure illustrating the participation of different cohorts in the group of individuals entering the population in a given year (Fig. 2 column 2 a and b), if not in every detail, then at least in combined percentages of the two generations.

Survival of individuals from different cohorts during winter (from October to April the following year) is very similar (Petrušewicz *et al.* 1971) and does not cause any important changes into the autumn age structure, apart from its even ageing by 6 months (Fig. 2 column 4 a and b). Thus in April following on a year »with a peak« the age structure is shifted towards individuals from the spring generation, which means, the population is older. $N(K_1+K_2) : N(K_3+K_4)$ in April following these years appears as 93 : 7 and 87 : 13, while in April following a year with »flattened« dynamics of numbers the younger individuals form a far greater percentage in the group of overwintered individuals and the above relation takes on values of 43 : 57 and 44 : 56. One year thus differs from another in respect of age structure of overwintered individuals, while their number remain basically the same.

It was found at the same time that when overwintered group characterized by old age structure enter upon the reproduction season its mortality during the course of this season is greater than when this group is characterized by a younger age structure (Fig. 3). Detailed analysis of this relation showed, that survival is not directly connected with the age of individuals, that is, is not age-dependent (Fig. 4)³. In such a situation the capacity for survival of individuals from the earlier cohort should always be lower than that of younger individuals from the autumn generation. The analysis made both for the whole group and for females only (as they are assumed to play the chief part in the viability of their progeny), however, showed that although in 1967 and 1969 (low population numbers, old age structure) the viability of the autumn generation is in fact better, in 1968 and 1970 (high population numbers, younger age structure of K_0) the reverse is the case. In addition, comparison of the survival curves for overwintered individuals originating from the spring generation, and separate analogical comparison for those originating from the autumn cohorts, showed that the viability of both groups is better in years when age structure is younger (April 1968, 1970) than in years when it is older (April 1967 and 1969).

³ As the age composition of the overwintered individuals in the spring of 1966 was unknown, it has been omitted from this analysis, and instead the group from 1970 was added. 1970 was a year in which the population was also distinguished by dynamics of numbers »with a peak« and was not subjected to any additional research operations during the period taken for analysis.

It would seem that the explanation of the relation found here between viability of overwintered individuals and their age structure must be sought in the social organization of the population. For instance it may be assumed that the social organization formed in the group when dominated by older individuals ($K_1 + K_2$), is less favourable (more sharply defined hierarchic relations, greater stress) and responsible for greater

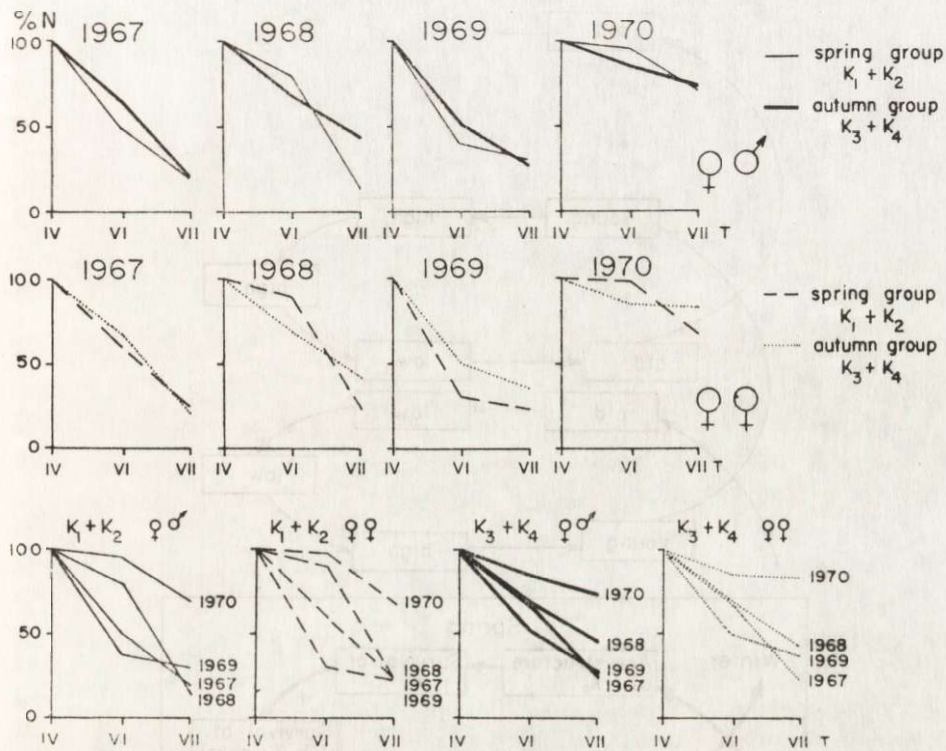


Fig. 4. Comparison of survival for the spring and autumn generation of overwintered.

mortality of individuals than is the case when there are fewer older individuals.

3. DISCUSSION

Population parameters discussed above: dynamics of numbers, viability of individuals belonging to different cohorts and age structure — indicate that a 2-year cycle occurs in the study population.

This cycle can take place through the following relations (Fig. 5): the older the age structure in the group of overwintered individuals

(K_0) the lower its viability; the lower the viability of K_0 (particularly in the early spring period when they form the core of the population; all females are pregnant and produce the whole K_1 and a large part of K_2) the poorer the viability of the young animals of the spring generation, during the period from 0–6 week of life (in accordance with the positive correlation found by Bujalska, 1975, between viability

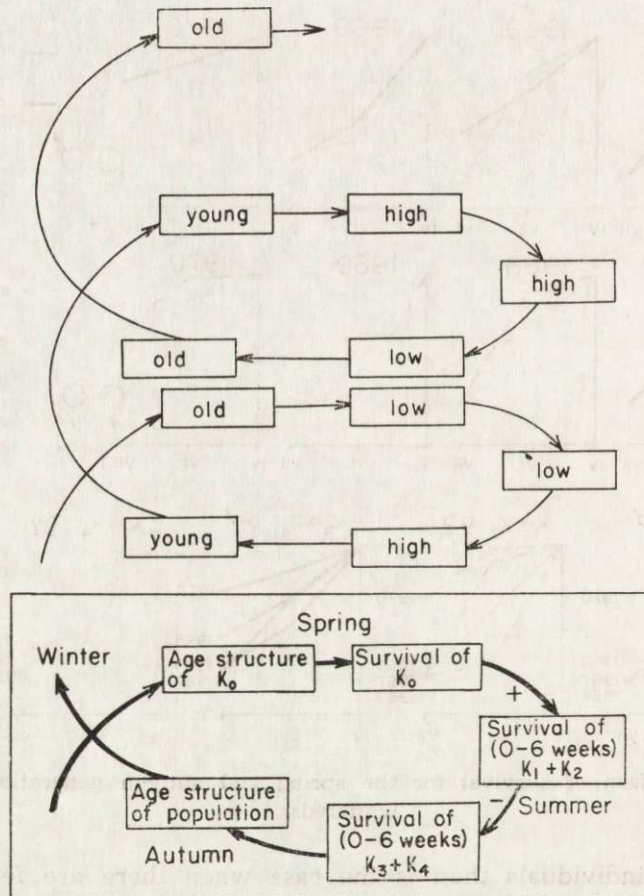


Fig. 5. Diagram of the way in which the two-year cycle takes place.

of young animals and viability of their mothers); the poorer the capacity for survival in this period of K_1 and K_2 , the better the capacity for survival during the first six weeks of life of individuals from the autumn generation (in accordance with the inverse relation between these processes to which reference was made above). Viability of individuals in these two groups: spring and autumn (with similar proportions from

year to year of individuals born in these periods) has a decisive influence on the age structure of individuals entering the winter period. As the mortality of all age groups is similar during the winter the above relation determines the age structure of the overwintered individuals (K_0) next year.

Thus if the age structure of K_0 is young (large percentage of K_3 and K_4) and their viability good, then the viability of the youngest K_1 and K_2 is good and viability of the youngest K_3 and K_4 low, and in effect the structure of the population is old in autumn and in spring the following year (large percentage of K_1 and K_2) and therefore its viability is low.

If the pattern described above is correct this means that the island population of bank voles is subject to endogenic rhythm. It is possible for this rhythm to become apparent in the population dynamics only when the exogenic factors affecting the population are constant from year to year.

The two-year cycle in dynamics of numbers has also been found by Koškina (1967) to occur in another species of vole — *Clethrionomys rutilus* (Pallas, 1779), although the way in which this cycle was fulfilled differed from that described above, as it was to a great extent dependent on variations in natality.

If relations similar to those described also occur (although are not clearly evident in the form of a regular cycle) in populations of other rodents, it is worth considering at which moment of such a cycle exogenic factors, especially those reducing or increasing the capacity of the habitat, may come into play. It seems as the inverse relation between the capacity for survival of the spring generation and autumn generation during the first period of their lives is this »sensitive point«. It is easy to understand that in a situation of abrupt increase in habitat capacity, with simultaneous low reduction during the nest period of the spring cohorts (resulting from the normal cycle of the population), individuals from the later cohorts also would have a good capacity for survival, causing rejuvenation of the age structure of the population in autumn not due to the cycle. This, in accordance with the above line of reasoning, would lead to high population numbers in the following year as well. And if increased habitat capacity continues over the winter period as well, then the survival of individuals through this period could be higher and the »basic stock« of the following year would be not only younger but more numerous, with consequences which are easy to foresee.

In order to understand fully the mechanisms responsible for realization of such a cycle it would be necessary also to explain certain other

relations, e.g. (1) in what way is the mortality of young depend on the mortality of their mothers (this question has been discussed in detail by Bujalska (1975); (2) what causes the relation between viability during the first period of the life of individuals from the spring generation (and therefore their numbers in the population at a later period) and viability during the first weeks of life of individuals from the subsequent generation, i.e., what kind of pressure do these individuals exert on each other; (3) in what way does the number (percentage) of older individuals in the group of overwintered voles determine the viability of the whole group.

There is finally one other question which arises and requires a better understanding of interaction between the population and external factors, namely, what are the causes and consequences for the population of maintaining a 2-year-cycle under habitat conditions which appear to be constant.

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STRUKTURA WIEKOWA I DYNAMIKA LICZEBNOŚCI WYSPOWEJ POPULACJI NORNICY RUDEJ

Streszczenie

Na podstawie materiałów pochodzących z czteroletnich badań wyspowej populacji *Clethrionomys glareolus* (Schröber, 1780), oraz opublikowanych prac opartych na tych samych materiałach, opracowano strukturę wiekową populacji i powiązano ją z dynamiką liczebności (Ryc. 1). Zbadano, w którym momencie życia populacji struktura wiekowa odgrywa rolę czynnika warunkującego dalszy rozwój populacji (Ryc. 2). Stwierdzono zależność pomiędzy strukturą wiekową a przeżywalnością przemyków w drugim roku ich życia (Ryc. 3 i 4), oraz odwrotną zależność pomiędzy przeżywalnością w pierwszym okresie życia osobników z generacji wiosennej i z generacji jesiennej (Tabela 1). Powyższe zależności w połączeniu ze znalezioną przez Bujalską (1975) pozytywną korelacją pomiędzy przeżywalnością osobników młodych a przeżywalnością ich matek, a także odmienną w różnych latach przeżywalnością osobników młodych z różnych generacji, pozwoliły na zbudowanie schematu realizowania się dwuletniego cyklu dynamiki liczebności populacji (Ryc. 5), dającego się dostrzec w wielu wskaźnikach populacyjnych.