the mature population and on their mortality. An analysis of the behaviour of this population "reserve" can provide information on the ways of compensation for the deviation from 1:1 the sex ratio in the entire population.

Using this approach, the categories of mature and immature individuals would be the axis of the structural division of the population, and the analysis of sex ratio in the cohorts making up these two categories would seem to be one of the most promising ways of obtaining insight into the mechanisms underlying the variablility of sex ratio in the population.

6.2. Age Structure

Joanna GLIWICZ

The age structure of a population at any given moment is the result of birth rate and death rate prior to this moment. It can be modified by migrations if there are differences in migratory tendencies among particular age classes. In turn, the age structure itself largely determines future birth rate and death rate. Therefore, knowing age structure, we can reconstruct some processes that have occurred in the population in the immediate past and also predict some future changes in its population dynamics. Consequently, it is not surprising that much attention is paid to this element in population studies.

It is not easy, however, to study age structure, especially in the wild. We can use one of two basic methods, but each of them serves slightly different purposes. Studying a poorly known population, we can use morphological and anatomical indices which vary with age and do not depend much on the condition of the animal. A critical review of such indices is given by Pucek & Lowe (1975) (see also section 2). The best indices of age in the bank vole are changes in the length of the roots of M_1 (Wasilewski, 1952; Pucek & Zejda, 1968) and changes in weight of the eye lens (Lord, 1959; Adamczewska-Andrzejewska, 1971). But to collect the material for calculating these indices, it is necessary to kill animals, and this is inconsistent with *CMR* methodology. Thus the age of living animals is determined from such indices as body weight or tail length, when their growth with age is known. These are very rough indices, however.

Another way of determining the age structure, but for a little different purpose, is based on the known population dynamics.

Under natural conditions such information can only be obtained by frequent recaptures of marked individuals. Knowing the approximate time of birth of each individual (in practice rather of a group of individuals — a cohort — which are assumed to be born at the same time), we can assess the age structure of the population at any time.

6.2.1. Changes in Age Structure

To characterize in the most general way changes in the age structure of bank vole populations it should be remembered that (1) these animals reproduce only in a breeding season of about six months (mid-March

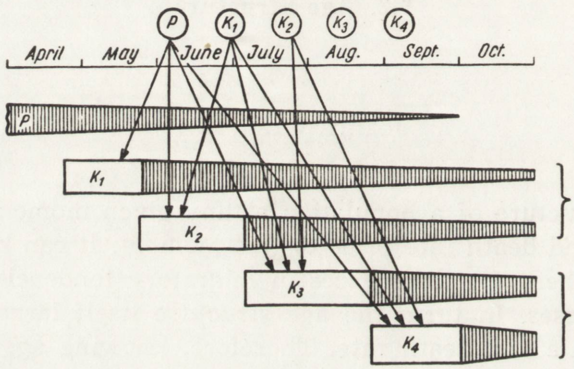

Fig. 6.3. Development of age structure over the breeding period. An island population, Poland.
P — overwintered individuals, K_1—K_4 — subsequent cohorts over the year. Arrows indicate the progeny of each cohort; G_w — spring generation, G_y — autumn generation.

of early April to late September) and (2) they bear many litters throughout the breeding period. Moreover, the turnover is so high in bank vole populations (low mean life span) that the difference in age among animals usually is not greater than one year, rarely 18 months.

The age structure of bank vole populations becomes completely changed over the six months of the breeding period. On the basis of the most general characteristics it may be stated that the bank vole population will be the oldest, that is, the mean age of individual voles in it will be the highest, in early spring, when it comprises only adults born in the preceding breeding period (overwintered). It will be the youngest immediately after the period of intense breeding, that is, when the number of the young is high and most of the overwintered voles have died. This is usually the case in summer or early autumn.

The sequence of changes in the age structure over the breeding period can be exemplified for an island bank vole population censused by the

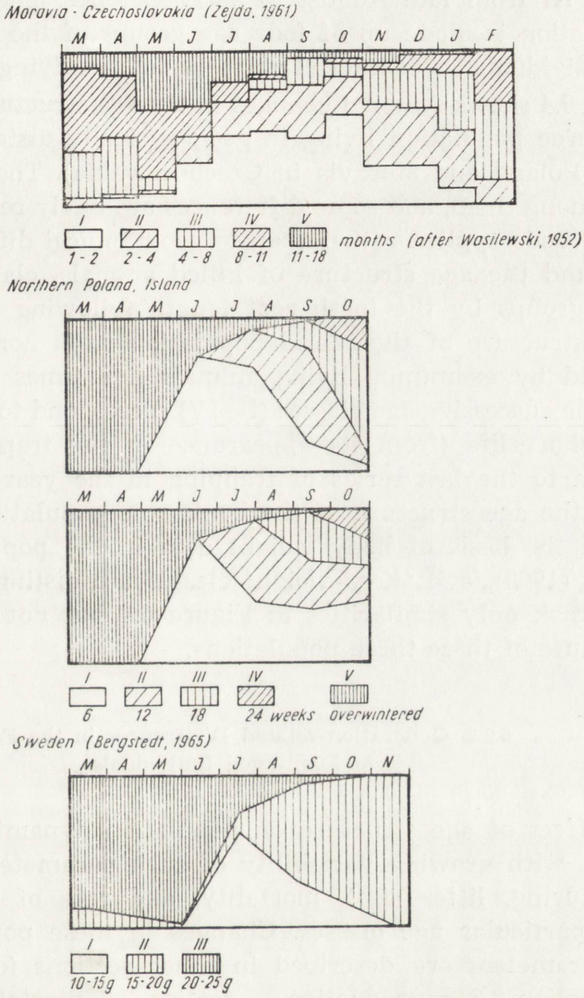

Fig. 6.4. Age structure of different bank vole populations. For explanations see the text.

CMR method (Fig. 6.3). Five age groups entering this population at different times of the season are distinguished. They consist of overwintered animals (K_0), and successive cohorts of the current-year animals (K_1—K_4)*. The first generation of the young (K_1) is born by overwintered animals in April-May and they become independent (enter the trappable population) in June. The next cohort (K_2) is born by overwintered and rapidly maturing K_1 voles in the period from the end of May to late July. Cohort K_2, in turn, gives birth, together with overwintered voles and cohort K_1, to cohort K_3 from July through August, and to cohort K_4 from late August to early October. Therefore, in autumn the population is made up of four age groups of the current-year voles and of individuals overwintered voles, which are dying out.

Figure 6.4 shows seasonal changes in the age structure of the trappable part of three population living in geographically distant areas (Sweden, northern Poland and Moravia in Czechoslovakia). There are great similarities among them, and some differences are likely related to differences in the methods applied rather than to geographical differentiation. Zejda (1961) found the age structure of killed animals, classifying them into five age groups by the tooth root length following Wasilewski (1952). The age structure of the island population from northern Poland was determined by examining living animals five times over the breeding period. The successive age classes (I—IV) correspond to successive periods in the cohort life (from its appearance in the trappable part of the population to the last series of trapping in the year of its birth). The graph of the age structure of the bank vole population in Sweden was drawn on the basis of body weight data in the population studied by Bergstedt (1965), and three weight classes are distinguished. Therefore, we can track only similarities in Figure 6.4 but not differences in the age structure of these three populations.

6.2.2. Generation-related Differences in the Fates of Even-aged Individuals

The effect of age structure on population dynamics and production increases with growing variability of such parameters as reproduction (e. g. maturing, litter size), mortality, and rate of individual growth between particular age classes. Changes in these population and individual parameters are described in other sections (changes in growth rate — section 2.3, reproduction — section 7.2, mortality — section 7.3). It is known, however, that the general characteristics of changes in

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* These cohorts are distinguished in an arbitrary way, based on the dates of successive series of trapping. All young voles captured for the first time during one of the trapping series are considered as a single cohort; the period of their birth determined along with the mean date of birth. Detailed descriptions of the history of cohorts, their characteristics, and the way of distinguishing them are given by Bujalska *et al.* (1968) and Gliwicz *et al.* (1968).

these parameters do not refer to all even-aged individuals in the population to the same degree as there are generation-related differences in individual growth and development.

The four bank vole cohorts distinguished above and which were born in the same breeding season, can be grouped in two essentially different categories: the spring generation comprising voles born in the first half of the breeding period (K_1 and K_2), and the autumn generation (K_3 and K_4). Some authors (Bobek, 1969; Zejda, 1971) have distinguished three generations, considering individuals born in midsummer as a separate group, but I will recognize two generations to enhance the contrast between their characteristics.

Bank voles born in the first half of summer grow faster than those born later. They reach maturity and reproduce in the year of their birth, in contrast to the voles from the autumn generation (Schwarz *et al.*, 1964; Bergstedt, 1965; Bujalska *et al.*, 1967; Gliwicz *et al.*, 1968; Kaikusalo, 1972; Zejda, 1971). As a result of intense growth, maturation, and reproduction their metabolism is much higher. According to Schwarz *et al.* (1964) and some others this may account for their higher mortality. Hence, the "duty" of more successfully surviving the winter and reconstructing the population in the next year would rest on the individuals born in autumn (Schwarz *et al.*, 1964; Kaikusalo, 1972). This view has not been supported, however, by the results obtained, for example, for an island bank vole population studied in Poland. Those results show that the autumn generation often survives worse than does the spring generation, and it usually does not form the bulk of overwintered animals (Gliwicz, *et al.*, 1968; Petrusewicz *et al.*, 1971; Bujalska, 1975a; Gliwicz, 1975; 1976). This discrepancy in views on the role of the autumn generation in bank vole populations may be related to climatic differences between the study areas. It may be expected that the additional energy expenditures for intense maturing and reproduction excessively burden the voles of the spring generation living under severe climatic conditions, thus already having high energy requirements and increased metabolism. For this reason they may live a shorter life and die during their first autumn in those areas. In the areas with less severe climate, the survival of the two generations follows a different pattern.

6.2.3. Age Structure in Overwintered Animals

Because individuals of the two generations differ in their characteristics, it is important to know their proportions in the population. The best time to ascertain this is at the end of the breeding period (end of October), when the youngest individuals have become independent. In this way we have access to the age structure of the population entering the winter period, and, at the same time, the age structure of overwintered animals, since it is generally agreed that winter mortality is independent of age. (see section 7.2). This simplified picture of age structure, with only two groups considered, is a very important population characteristic, which allows conclusions on population dynamics from knowledge of the possible fates of individuals belonging to these groups, and which enables comparison of different populations or the same population in different years.

For example, the age structure of the island bank vole population discussed above was markedly different in autumn (October) for two successive years (Fig. 6.4). Analogous differences occurred in the age structure of overwintered animals (Fig. 6.5). In the spring of 1967, the

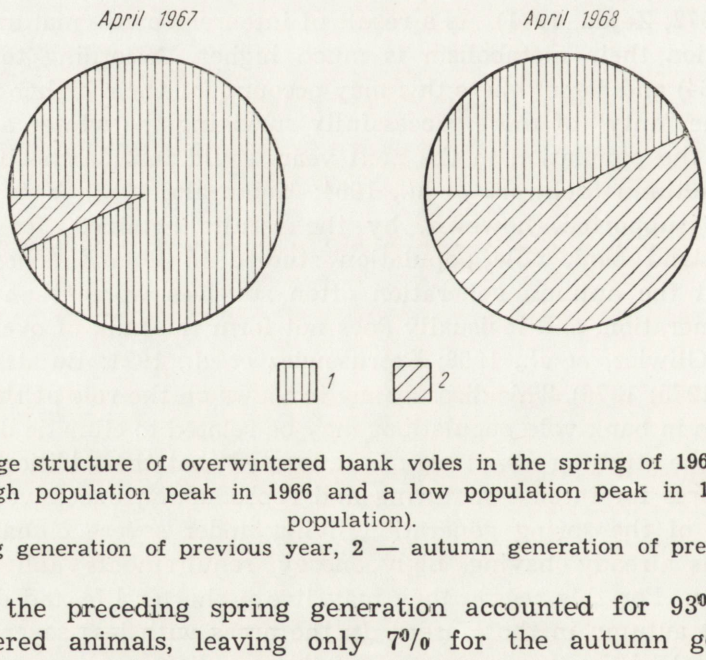

Fig. 6.5. Age structure of overwintered bank voles in the spring of 1967 and 1968 after a high population peak in 1966 and a low population peak in 1967 (island population).
1 — spring generation of previous year, 2 — autumn generation of previous year.

voles of the preceding spring generation accounted for 93% of the overwintered animals, leaving only 7% for the autumn generation. The respective figures in the spring of 1968 were 43 and 57%. What can be said from this about past and future fates of the population? In 1966, the net production (number born minus nestling mortality) in spring must have been much higher than in autumn. This difference was probably even greater than indicated by the age structure in autumn or spring of the following year because the voles born in spring, being older, were subject for a longer time to the action of different mortality factors. Therefore, in 1967, the group of overwintered animals was relatively uniform (with a small admixture of autumn generation). It consisted mostly of individuals that reproduced in 1966. Moreover, most of these voles were born and grew under similar climatic and habitat conditions, characteristic of the first half of the breeding season. Finally, it may be suggested that the social hierarchy was relatively well developed among those individuals because a large number of them reached independence simultaneously, and tried to find their places in the spatial and social structure of the population at approximately the same time. Such situations should enhance a strong dominance structure. In turn, in 1967, the spring generation increased slower than in 1966, thus more or less at the same rate as the autumn generation. Recruitment of young must have been similar for these two generations. The population of overwintered animals in the spring of the following year was, however, more diversified. It comprised individuals that had reproduced the preceding year as well as individuals just reaching maturity. It is probable that social relationships among them were less antagonistic. As a result, the overwintered animals survived better in 1968 (Gliwicz, 1975) and their offspring survived better as well (Bujalska, 1975a). This generated higher population numbers in that breeding season, to a different age structure, and thus changes in other population parameters.

Cyclic changes in the age structure of overwintered animals in bank vole populations, and the effects of these changes on population dynamics have also been recorded by Zejda (1967) and Pucek & Pucek (in litt.). Also Hansson (1969a) observed that in the year of a high population density, the overwintered animals were youngest, while in the year of a low population density they were oldest (more than half were recruited from the first spring litters of the preceding season). All these observations suggest that the population age structure can be a component of intrapopulation mechanisms of number regulation, thus determining population level.

6.3. Spatial Organization of the Population

Maria MAZURKIEWICZ

According to Naumov (1956), bank voles live singly or in families, and spatial structure of their populations as well as forms of individual interactions are realized through a system of home ranges. A general