

7. DYNAMICS AND REGULATION OF THE POPULATION

7.1. Patterns of Population Dynamics

Kazimierz PETRUSEWICZ

Population dynamics, that is, changes in the number of individuals with time, sums birth rate, death rate, emigration, and immigration. Emigration and immigration have been discussed above (section 6.4). Population dynamics of the bank vole seem to depend on emigration and immigration under some special circumstances. I do not know about macroimmigration or macroemigration of the bank vole. Macroimmigration in the bank vole is only a logical postulate: this widely distributed species must have expanded into new areas. Population dynamics of this species greatly depend on the birth rate and death which will be discussed in more detail below (section 7.2 and 7.3). Here, in this introduction to the section on population dynamics I will present only necessary general ideas.

Bank voles breed during the growing season (for details see section 7.2).

The biological year of the bank vole lasts from one spring to another, in England, for example, from March to March, and in Poland from April to April. In Poland, April is the time of minimum numbers in most cases, as on young are born in autumn, winter and spring, and the animals are only dying out. This lowest standing crop — the number of individuals starting breeding and as a result ensuring the continuity of the population — is usually called the basic stock. In April mating begins, the first pregnant females appear, and the first young are born (this will be discussed in detail in section 7.2). As the birth rate is higher than the death rate, the population increases rapidly, reaching a peak in July-October, as is shown in Figures 7.1, 7.2 and 5.1 (Andrzejewski, 1963; Petruszewicz *et al.*, 1971; Gliwicz, 1975; Bujalska, 1975b). Then the population declines until April resulting in a sinusoid-like pattern shown in Figures 7.1, 7.2, and 5.1.

Bank voles live in well-balanced populations. A more detailed analysis was made for 31 populations. A total of 139 maximum/minimum ratios were calculated, and an average of 4.7 was obtained. One max/min ratio was higher than 60, two were higher than 20, and three

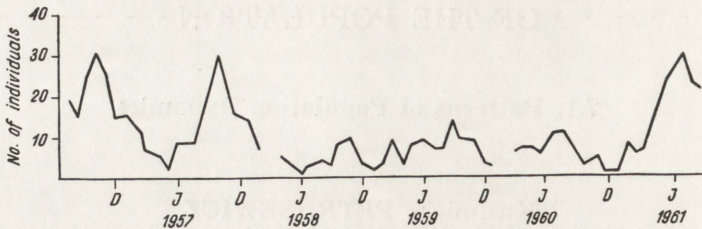


Fig. 7.1. Population dynamics of bank voles in the Kampinos Forest. Average numbers per month per 4 ha are given.
D — December, J — June (after Andrzejewski, 1963).

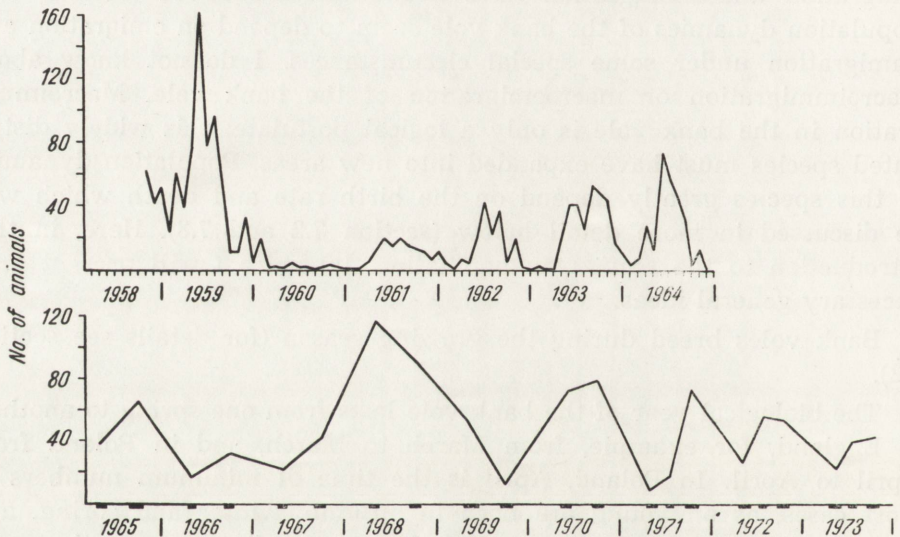


Fig. 7.2. Population dynamics of bank voles in the Białowieża National Park (1958—1973).

(after M. Pucek & Z. Pucek, unpublished data).

ratios exceeded 10. Peak numbers most frequently exceeded the spring minimum about 5—6 times. Generally, populations of forest rodents are much more stable than the populations living in open habitats such as meadows, steppes, or semi-desert (Golley *et al.*, 1975b). But even among forest populations, the bank vole population seems to be more stable than populations of other rodents associated with forests.

As far as seasonal fluctuations are concerned, usually the size of

the basic stock, starting breeding in April, is much more stable than peak numbers. During the four-year study on Crab Apple island, the maximum basic stock was 1.2 times as high as the minimum basic stock, and the corresponding figure for the highest and lowest peak numbers was about three times (Petrušewicz *et al.*, 1971; Gliwicz, 1975). In the four-year study carried out in the Niepołomice forest, the ratios of highest/lowest basic stock were 3.2, 2.6, and 1.3, while the corresponding ratios for peak numbers varied from 5.0 to 22.0 (Bobek, 1973).

It should be added here that in absolute numbers (not as max/min ratio), maximum numbers often show larger fluctuations than minimum numbers. For instance, during the four-year study period on an island population inhabiting lake Beldany, the lowest and highest minima

Table 7.1.
Variable and stable parameters of population size on a 4-ha island
(after Petrušewicz *et al.*, 1971).

Parameters	1966	1967	1968	1969	CV %
Peak numbers	304	201	399		27
Time of peak	July	Sept., Oct.	July		
Daily survival K_1	0.81	0.79	0.48		22
in percent of N K_2	0.32	0.56	0.83		37
Number born (v .)	1048	1090	1011		3
Production (P) g live wt./4 ha/year	11429	11714	13061		6
Basic stock, April	56	68	70	62	6

ranged between 14.5 to 17.5 individuals per ha; thus the annual fluctuation was 3 individuals/ha. Maximum numbers, however, varied from 50 to 75 individuals per ha; thus the difference was 25 individuals/ha. This gave rise to a concept (Petrušewicz *et al.*, 1971) that in the population there are constant and variable parameters (Table 7.1). The constant parameters involve the size of the basic stock, production, and the number of born over a year. So far this concept has not been empirically confirmed.

Bank vole populations, like populations of other species, show an interesting property: closed populations are more dense than open ones; at the same time, their density increases with decreasing size of the isolated area occupied by the population (Petrušewicz, 1963, 1978; Petrušewicz & Uchmański, 1980).

The first attempt to explaining this phenomenon was made by Petrušewicz (1963, 1978). A detailed explanation was suggested by Petrušewicz & Uchmański (1980), and is summarized below. According to Krebs *et al.*, (1969), higher densities of confined populations are due to the lack of migration. This may be a logical explanation with some additional reasoning.

Both emigration and immigration should be considered here. In closed populations both processes are nonexistent. The confinement of a population can account for an increase in its density only if in corresponding open populations emigration outweighs immigration. This is likely to be the case because migrating individuals are subject to heavier mortality than residents, as has been shown in studies carried out at the Institute of Ecology, PAS (see section 6.4). This implies that at any average site, emigration must be higher than immigration. In view of this fact, the density of a closed population, with no emigration and immigration, should increase not as an effect of the absence of emigration alone but as a result of the absence of an excess of emigration over immigration.

But the absence of emigration may be only one of the reasons for an increase in density. Density also increases when isolation is not complete. Islands, wooded areas scattered in croplands, and urban parks are all examples of partly isolated habitats. It can be assumed that the probability of encounters between individuals (interference) will be lower in a closed population than in an open one. In an isolated space only the individuals inhabiting this space can encounter. In an open space — assuming that this space can be covered by individual animals in a short time — the number of encounters with neighbours and with neighbours of the neighbours increases; hence, the interference is stronger, and the effects of crowding can intensify, with a consequent decrease in density. Differences in the number of contacts among individuals in closed as compared with open populations explain also what was not noticed by Krebs *et al.* (1969), who also explained why the densities of closed populations increase with declining space inhabited by these populations.

7.2. Reproduction

Gabriela BUJALSKA

7.2.1. Methods for Estimating Birth Rate

Birth rate as expressed by the number of individuals born per unit of time is, along with death rate and migration, a basic component of population dynamics. Birth rate depends on the number of pregnant females, litter size, and duration of pregnancy (Bujalska *et al.*, 1968).