

## 5. NUMBERS: THE CONCEPT AND DEFINITIONS

### 5.1. Numbers and the Number of Discrete Individuals, Turnover

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Numbers ( $N$ ), also called densities, have been defined as the number of individuals per unit area at a given time (at the time of sampling). These terms also refer to the number of individuals per sample, or, sometimes, to the number of individuals in the population independent of the size of the area occupied by this population. For animals of the size of the bank vole, numbers ( $N$ ) are usually defined as the number of individuals per hectare.

Numbers of bank voles, like any other species, fluctuate in time. There are seasonal (phenological) changes in numbers and annual changes. I shall discuss them in more detail in section 7.1.

The graph of numbers ( $N$ ) on the time axis is a characteristic curve called the curve of population dynamics (Figs. 5.1, 7.1, 7.2). The curve on Figure 5.1 illustrates seasonal changes in population dynamics.

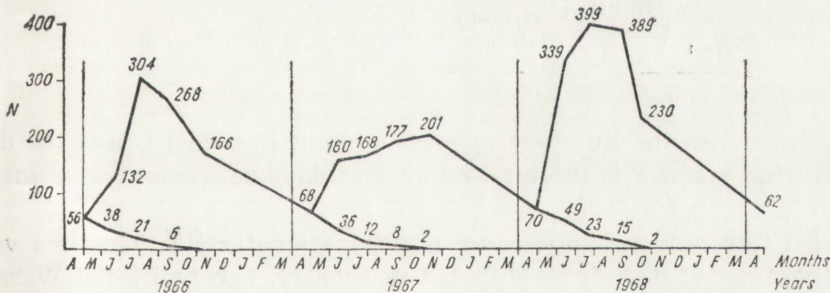


Fig. 5.1. Population dynamics ( $N$ ) of the bank vole on a 4-ha island (from Petruszewicz *et al.*, 1971).

Numbers ( $N$ ) are a basic ecological parameter. In populations containing different categories of individuals (males and females, young and adults, pregnant and lactating females, light and heavy individuals, etc.), numbers are the starting point in calculating other ecological pa-

rameters. Thus, in the next section (5.2) I discuss the methods of estimating numbers and their reliability.

Knowing population dynamics in one or more localities over the year or several years, we may be interested in mean numbers ( $N$ ) per year, or per growing season versus winter period, or per any other period of time. Mean density has been defined (Petrušewicz, 1966b; Petrušewicz & Macfadyen, 1970) as

$$\bar{N}_a = \frac{1}{k} \sum_{i=1}^{i=k} N_i \quad 5.1$$

where  $k$  is the number of measurements (records) and  $N_i$  denotes successive population numbers. Note that records should be distributed more or less evenly in time. It is frequently the case that we have many records over the growing season, when  $N_i$  is high, and few records in winter (e. g. for technical reasons), when  $N_i$  is low, and, consequently, the average value will be overestimated. This issue is analysed in detail by Petrušewicz & Macfadyen (1970), who pointed out that the calculated unweighted average value can be twice the weighted average value (see Fig. 5.2). The best way to avoid this error is to calculate the area under the curve of population dynamics. This can easily be done by summing the areas of figures between successive measurements (Fig. 5.2). Obviously, in this way we will get the value of  $\bar{N}T$ , where  $\bar{N}$  is an average number over time  $T$ . The weighted average can be calculated from the formula

$$\bar{N} = \frac{\sum_{i=1}^{i=k} \left( \frac{N_i + N_{i+1}}{2} \right) (t_{i+1} - t_i)}{T}$$

where  $N_i$  denotes the numbers in measurement (records)  $i$ ,  $t_i$  is the date of measuring  $i$ , and  $T$  is the total number of days between measurements  $i$  and  $k$ .

I wish to stress the importance of the parameter  $\bar{N}T$ . This is a very useful parameter, though rarely used in ecology, except by the Warsaw School of Ecology (Petrušewicz *et al.*, 1969, 1971; Petrušewicz & Macfadyen, 1970). The value of  $\bar{N}T$  indicates the number of individual-days in period  $T$ . Therefore, this is the number of individuals that exert a pressure on the environment through their consumption of food, or this is the mass of individuals available for predators; this is also the number of reproducing individuals. The parameter  $\bar{N}T$  provides a more comprehensive characteristic of the population than  $\bar{N}$ .

But neither average numbers,  $\bar{N}$ , nor the number of individual-days,



$\bar{N}T$ , nor the curve of population dynamics characterize the number of individuals present in time  $T$ . If, for example, there were 10 individuals at time  $T_1$  and 25 individuals at time,  $T_2$ , this might be a result of the input (birth, immigration) of 15 individuals, with no elimination (death, emigration), or of the input of 30 and elimination of 15 individuals, or even the input of 100 individuals and elimination of 75. The real number individuals ( $\nu$ ) present in the population over the study period  $T$  is given by the formula

$$\nu + N_o = \nu_r \tag{5.2}$$

where  $N_o$  is the initial number, and  $\nu_r$  is the number of individuals born. The total balance of the number of individuals over time  $T$  can be calculated as

$$N_T = N_o + \nu_r - \nu E \tag{5.3}$$

where  $N_T$  is the number of individuals present in the population in time  $T$ ,  $N_o$  is the initial number of individuals, and  $\nu E$  is elimination (death, emigration). This formula can also be written

$$\nu_r = N_T - N_o + \nu E = \Delta N + \nu E \tag{5.4}$$

The number of individuals born ( $\nu_r$ ) represents population production expressed in the number of individuals.

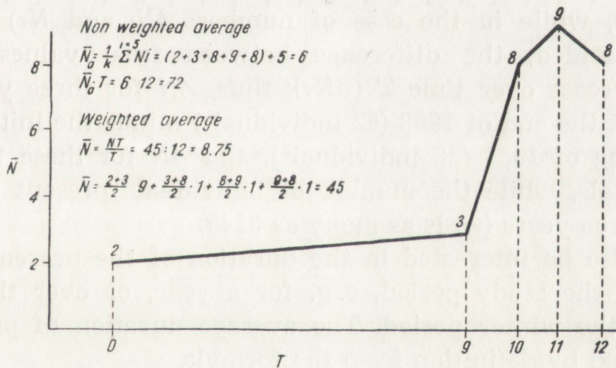


Fig. 5.2. Average numbers ( $\bar{N}$ ) properly averaged.

For a short time period, usually  $\nu_r = \Delta N + \nu E$ , but for a longer period, e. g. for a year, or for a reproductive period,  $N$  differs little from elimination so that we can write

$$\nu_r \approx \nu E \tag{5.5}$$

I will illustrate this relationship using the data from Crab Apple island on lake Beldan (Mazuria, Poland), which is inhabited by the most

thoroughly studied free-living population of the bank vole. The data calculated from Petruszewicz *et al.* (1971) show the individual budget from April to April (biological year for the bank vole) over three years (Table 5.1).

Table 5.1

Annual balance (April to April) of individuals in the bank vole population on Crab Apple island over three years (after Petruszewicz *et al.*, 1971).

	$\nu_r = N_T - N_0 + \nu E = \Delta N + \nu E$
1966	$1048 = 68 - 58 + 1038 = 10 + 1038$
1967	$1090 = 70 - 68 + 1088 = 2 + 1088$
1968	$1011 = 62 - 70 + 1019 = -8 + 1019$
1966—68	$3149 = 62 - 58 + 3145 = 4 + 3145$
Average/year	$1049 = 66 - 65 + 1048 = 1 + 1048$

As it can be seen from this table, the difference between the initial and final numbers over a year equals to 0.2—1% of the elimination, while the average for three years equals to 0.01% of the elimination. Thus, I do not make a great error if I omit the term  $\Delta N$  in formula (5.4) and use formula (5.5) instead.

It should be noted that the values of  $\nu_r$  and  $\nu E$  can be added for any period of time, while in the case of numbers ( $N_t$  and  $N_T$ ) only final values can be added; the difference between final values gives an increase or decrease over time  $T$  ( $\Delta N_T$ ); thus,  $\Delta N$  for three years is the final number at the end of 1968 (62 individuals) minus the initial number at the beginning of 1966 (58 individuals), and  $\Delta N$  for these three years is +4 individuals, while the number of individuals present in this population for three years ( $\nu_r$ ) is as many as 3145.

One may also be interested in the duration of the presence of individuals during the study period, e. g. for a year, or over the growing season versus the winter period. The average duration of presence ( $\bar{t}$ ) can be calculated by definition from the formula

$$\bar{t} = -\frac{1}{\nu} \sum_{i=1}^{i=\nu} t_i \quad 5.6$$

Note that the duration of presence over time  $T$  does not equal the length of life: this is the length of life but only in the study period  $T$ , e. g. from April to April; the duration of presence of the animals entering their next reproductive season after winter is considered only by April (for the period April-April); hence, the average duration of life is a little longer than the average duration of presence.



An interesting parameter is

$$v\bar{t}' = \sum_{i=1}^{i=\nu} t_i$$

Obviously,  $v\bar{t}'$  is the number of individual-days over time  $T$ . I have indicated above that  $\bar{N}T$  is also the number of individual-days in time  $T$  (Petrušewicz, 1966b; Petrušewicz & Macfadyen 1970), thus

$$\bar{N}T = v\bar{t}' \quad 5.7$$

This equation can be of great importance as the parameter  $T$  can be arbitrarily selected, parameter  $\bar{N}$  can be relatively easily found empirically, while the number of individuals ( $\nu$ ) and the time of presence ( $\bar{t}'$ ) are much more difficult to determine empirically. Thus, if we have one of these parameters, we can easily calculate the other one from equation 5.7. This equation, however, should be used cautiously; e.g. it is usually impossible to calculate  $\nu$ , because  $\bar{N}$  and  $\bar{t}'$  are calculated for individuals that survived until the so-called trappable age.

Let me note that  $\nu/\bar{N}$  says how many times average numbers have been exchanged over time  $T$ , this is turnover as expressed by the number of individuals ( $\Theta_N$ ) (Petrušewicz, 1966b).

$$\Theta_N = \frac{\nu}{\bar{N}} = \frac{T}{\bar{t}'} \quad 5.8$$

And if  $T$  is a unit time (e.g. a year) and this unit is used as a measure of  $\bar{t}'$ , we will get

$$\Theta_N = \frac{1}{\bar{t}'} \quad 5.9$$

Individual turnover ( $\Theta_N$ ) is similar to but not identical with biomass turnover. We will discuss differences between these two concepts in Chapter 8 after discussing biomass turnover.

Equation 5.7 shows that numbers (standing crop) depend on both the number of individuals and the time of their presence:  $\bar{N} = v\bar{t}'/T$ . Two examples illustrate this.

A removal experiment was carried out in the Kampinos Forest (Andrzejewski & Wrocławek, 1962). As a result of intense trapping, a 4-ha "rodent vacuum" was created. Then the recolonization of this vacuum was observed. It has been shown that the immigration rate was not higher than in the other, undisturbed area. However, more rodents settled there and the duration of settlement increased. As a result, numbers of animals on the experimental plot rapidly increased to the level characteristic of adjacent areas. This increase in numbers

was due to the increase in the time of presence ( $\bar{t}$ ), and not due to the increase in the number of immigrants ( $\nu_{im}$ ).

Another example: in most cases both in the field and in the controlled laboratory experiments the number of young is lower than the number of adults. This results from the fact that a young individual (arbitrarily, up to seven weeks old) can be present at most seven weeks, and then it becomes adult; as an adult it can be present for 18 months.

## 5.2. Numbers — Methods of Assessment

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### 5.2.1. Capture Techniques

The methods for the assessment of bank vole numbers do not differ from those applied for number estimation of other small rodents. Thus we will only enumerate them here, and indicate what additional information we can get using these methods, without going deep into their advantages and shortcomings. Those interested in the technique of calculations or in the comparison of various methods are referred to Smith *et al.* (1975).

The cases when numbers or density can be determined by the removal of all or almost all individuals living in a given area are rare and limited to isolated populations, e. g. on islands (Andrzejewski *et al.*, 1967; Gliwicz *et al.*, 1968), artificially isolated (Gębczyńska, 1966), or confined. Long-term trapping from open areas can lead to the so-called complete removal, despite disturbance caused by immigrants, but the extent of the "vacuum" produced is not exactly known (Andrzejewski & Wrocławek, 1962; Kozakiewicz, 1976).

Indirect methods such as tracking on snow provide only rough approximations of vole numbers as the activity of these animals on the surface of snow cover largely depends on weather and snow quality (Rotshild, 1959). Strongly ramified burrow systems of the bank vole do not allow the application of flooding (Truszkowski, personal communication). For these reasons we estimate numbers from samples of individuals caught in a given location. Most frequently, bank voles are caught on sampling areas or on trap-lines with a specific configuration