

birth rate, compared with large changes in the population size, could be interpreted as being inversely proportional to the population density if, for instance, the proportion of mature or breeding females is analysed. In fact, birth rate is stabilized by spatial interactions between mature females, thus is independent of the population size.

The same concerns the survival (mortality) of the young. In the first half of the breeding season, population density depends on changes in mortality, and not conversely. Only in the second part of the breeding seasons mortality is likely to be density-dependent. But this issue requires further investigation.

7.3. Survival and Life Span

Joanna GLIWICZ

Death rate and birth rate are primary factors determining population dynamics. The literature analysing the role of these processes contains controversial views concerning their variability and relative importance to the ultimate character of population dynamics. The purpose of this paper is to characterize general patterns of mortality in the population of a typical rodent associated with forests of the temperate zone, and also to describe factors affecting this process as a whole especially the lives of individual animals and the population. Against this background, the role of mortality as a factor regulating population numbers will be indicated.

7.3.1. Mortality Patterns in Bank Vole Populations

Analysing mortality in populations of relatively short-lived mammals, it is easy to distinguish periods of different mortality in individual life and in phenological cycles of the population. Published data usually treat mortality in such distinct periods. Thus also in this paper four periods are distinguished.

Nesting Period or the Period of Dependent Life

It is generally assumed that young bank voles remain in their nests for about 21 days, and then they begin an independent life. A little later they begin to search a sufficiently large area and they attain

a sufficient weight to be trapped. Only after this is it relatively easy to obtain direct information on their numbers and survival. All data concerning the earlier period are indirect estimates. For this reason the term "nesting period" covers here a considerably longer period than the actual nesting period does. For example, in the case of an island

Table 7.5
Survival of the bank vole as estimated by different authors.

Per cent survival in nesting period			Average
39—53% per 1 month	depending on the cohort	Ryszkowski & Truskowski, 1970	
60% per 1 month	spring cohort		
68% "	summer cohort	Bobek, 1973	$S = 47\%$
31% "	autumn cohort		per month
37% per 6 weeks	only females	Bujalska, 1975a	or $\mu = 0.025$
			per day
35% "	4-year mean for 4 cohorts maximum differentiation, island population	Gliwicz, 1975	
61—10% "	newborn surviving till maturity		
42% ca 2 months		Radda, 1968	$t = 42$ days
Independent individuals — the 1st summer			
60% per 1 month	only females	Newson, 1963	
80—60% "		Smyth, 1968	$S = 70\%$
66—80% "		Bobek, 1973	per month
65% per 6 weeks	average for island population	unpubl.	$\mu = 0.012$ per day
59—72% "	only females	Bujalska, 1975a	
70% ca 1 month	old subadults reaching maturity	Radda, 1968	$t = 75$ days
Winter period			
85% per month		Chitty & Phipps, 1966	$S = 85\%$
80—86% per month		Newson, 1963	per month
80% per month		Smyth, 1966	$\mu = 0.005$ per day
83—85% per 6 weeks	only females	Bujalska, 1975a	$t = 180$ days
87—89% per month		Petrusewicz <i>et al.</i> , 1968	
Overwintered individuals in their second summer			
75% per 6 weeks	first half of winter		first half
30% "	second half of winter	Gliwicz, 1975	$S = 80\%$
			per month
100—80% per month	first half of winter		$\mu = 0.007$ per day
50—40% "	second half of winter	Chitty & Phipps, 1966	
89—75% per month	first half of winter		second half
66% "	second half of winter	Newson, 1963	$S = 40\%$
			per month
60—50% per month		Smyth, 1968	$\mu = 0.031$ per day
58—51% per 45 days	only females	Bujalska, 1975a	$t = 90 + 90$ days

population on Beldany lake, the nesting period is considered to extend for 42 days (Table 7.5). Probably, however, non significant error is committed by pooling nesting mortality *sensu stricto* and the mortality shortly after weaning. The first weeks, and particularly first days of life of all mammals are characterized by low survival. It may be assumed that their mortality shortly after weaning is also high.

Data on survival in the wild population in this initial period are generally obtained by one of the two methods. One method uses indirect estimates of birth rate; the number of individuals born is estimated and this is then compared with the number of individuals trapped after some time. Obviously, the accuracy of this estimate of survival depends on the accuracy of the estimate of the number of newborn and on the time interval between parturition and the date of first capture, thus on the age of captured individuals. The other method uses data on the survival of individuals marked soon after their birth, the individuals surviving through the trappable age being counted. Usually the animals are marked in Howard's (1949) nest boxes that can easily be inspected. The accuracy of this method depends on whether a sufficiently large and representative group of young is marked, and whether or not the assumption is true that the animals living in artificial nests and marked in the first days of their lives survive as well as non-experimental individuals of the same age. This depends on incidences of cannibalism or abandonment by their mother, frequency of movement to another nest, etc. In the studies on the bank vole, this method was used by Ryszkowski and Truszkowski (1970).

Independent (Trappable) Individuals in the Year of their Birth

This is the most heterogenous group of all the groups considered. Members of this group differ by age (1.5—6 months on Crab Apple island), by reproductive condition (immature, maturing, and mature), and probably by some physiological or genetic properties as they were born in different periods of the breeding season. In the literature, however, most frequent were data on the survival of individual voles over the breeding season, and the great majority of them are mature animals older than three months. A few papers analysing particular periods or subgroups of individuals in this group are descriptive, with no quantitative data. Three papers will be discussed later, and here this heterogenous group will be considered as a whole to obtain the most general pattern of survivorship.

A difficult issue at this point is the length of the period for which this general mortality can be estimated. The time of individual life is

superimposed on the phenological time, and individuals born early in the breeding period live under "summer" conditions for six months, this being the mean length of the growing season in Europe within the range of the bank vole distribution. Of these six months, they join the group of "independent" animals for 4.5 months, on the average (from 1.5 to 6 months). But animals born at the end of the growing season live zero months under summer conditions. It has been assumed that an average individual of this group lives equally long as an independent individual in its first growing season, that is, for about 2.5 months. This is the mean value $(4.5+0):2$ slightly modified on the assumption that slightly more individuals are born during the first half of the growing season.

Data on survival in this period and in all other periods are obtained by persistent recaptures of marked individuals (CMR) or by snap trapping (e. g. SM). In the first case, survival can be estimated from the number of individuals present at time t that survived to time $t+1$. The accuracy of this estimate depends on the duration of period $(t+1) - t$ and on the turnover of individuals as a result of migration. When the second method is used, survival is estimated by comparing age structures of the captured part of the population at time instants t and $t+1$. In this case the estimate of population dynamics is based on the assumption that the area from which all the animals have been removed by trapping is then colonized by individuals with the same ecological characteristics.

Winter period. It has been assumed that winter extends for 6 months (November 1—April 1). The literature data concerning winter survival are extremely consistent. Particular emphasis is on the fact that the group of chronologically and physiologically differentiated individuals becomes homogeneous with respect to survival upon entering the winter period. It is frequently assumed that mortality is constant over the whole 6-months period. Distinguishing this period for the purpose of estimating survival is very simple and useful.

Overwintered animals (the second breeding season). Overwintered animals are a rather homogeneous group. All of them are mature and relatively advanced in age (7—12 months old). But a more detailed analysis shows some differentiation within this group, which will be discussed later on. This differentiation, however, does not seem to affect the general pattern of survival in this period of life. Mortality of this group tends to increase during the 6 months of the breeding season, and many data imply that clear differences in mortality occur at least at the beginning and at the end of the second breeding season of these animals. Therefore, this season has been divided into two three-month periods that differ in mortality of overwintered animals. The

transition between these two periods is probably gradual. The number of individuals surviving beyond the end of the second growing season is so low that their further fates cannot be statistically described. It is only known that the oldest individuals living in wild populations were born in early spring of the preceding year and they died in late autumn of the following year at an age of 18 months (Sviridenko, 1966; Gliwicz *et al.*, 1968; Pucek *et al.*, 1968; Petruszewicz *et al.*, 1971). Single individuals survive in addition through a part of winter, thus 20—21 months (Zejda, 1961; Pucek *et al.*, 1968). Stein (1956) captured one individual (of $700 = 0.14\%$) which survived two winters. Bank voles surviving two winters are also known from an island population in northern Poland (Andrzejewski, personal communication). They were probably born at the end of the preceding breeding season, thus they were not more than 20—21 months old. These are sporadic cases, however.

Table 7.5. contains numerical data and statements indicating general trends. Since different authors used various indices of survival and various time units (per day, months, or six weeks), their were transformed for comparative purpose. Such indices have been calculated as the mean

percentage survival $\frac{N_t}{N(t+1)} \cdot 100$ over one month, and the rate of the

elimination of individual animals, μ , as calculated from the formula $N_{t+1} = N_t e^{-\mu t}$ for $t = 1$ day. These indices are used to characterize individual survival in each of the periods distinguished.

On the basis of these indices and taking into account the length of particular periods, a general survivorship curve has been obtained, which characterizes the rate of elimination from an average population living under "average" climatic and food conditions, in a year of average numbers (Fig. 7.8).

Generally, this curve is strongly concave. It shows that as many as 65% of the young bank voles disappear from the population before they can be recorded by trapping, that is, when they are less than 6 weeks old; additionally, 20% disappear in the growing season, and only 15%, which enter winter diapause, have a chance to survive some part of the following breeding season.

7.3.2. Factors Determining Survival in Different Periods

Nesting period. At this age mammals face difficult physiological changes, e. g. the development of thermoregulation, which in the bank vole is "completely developed" on day 19 after birth (Gębczyński, 1975), or the transition from milk to solid diet. It has also been found (Buchalczyk, 1970) that the mortality of these young significantly

increases when their mother delivers another litter after the post-partum oestrus and before the young of the preceding litter become independent. A high mortality of the young during the nesting period is also related to such casual events as the death of a lactating female, flooding the nest, or the pressure of specialized nest predators such as vipers or weasels. As a result, generally entire litters die.

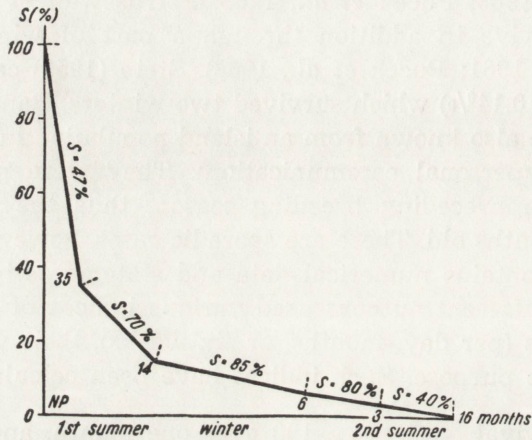


Fig. 7.8. Survival of the bank vole (mean values, according to different authors, see Table 7.5).

NP — nesting period = 42 days, S — survival in per cent per month.

In general nesting mortality of the bank vole is very high, reaching 60—70% during the first six weeks of life. A slight decrease in this mortality can significantly increase the level of population dynamics. Many authors show that the survival of the young in the first period of life depends on the time of birth and on the phase in the population cycle. Generally, young born in the first half of the breeding season survive the nesting period better than those born in the second half (Bujalska, 1975a; Gliwicz, 1975). Authors distinguishing three generations over the breeding season found that the voles born in mid-summer survive best (Zejda, 1961; Ryszkowski & Truszkowski, 1970; Bobek, 1973). Differences in survival related to the time of birth may result from changes in the habitat-food conditions over the breeding season, and also they may be due to the increasing population numbers towards autumn, causing stronger individual interactions and increased intraspecific competition. These factors always most severely affect the youngest individuals in the population.

Mortality of these individuals over the annual cycle also depends on the phase in the population cycle. An island population of voles experienced a two-year cycle over a four-year study period (after

a year of high numbers there was a year of low numbers), the number of born being identical in the two years (see section 7.1, Bujalska, 1970). The young born in the first half of the year of high population numbers survived much better than those born in the year of low numbers (Table 7.6), and the opposite was true of the survival of individuals

Table 7.6

Survival of the youngest individuals (0—6 weeks old) in the bank vole population relative to the time of birth (after Gliwicz, 1975).

h — high population numbers, l — low population numbers.

Year	Spring generation S (%o)	Autumn generation S (%o)	Spring generation/ autumn generation
1966 (h)	53.7	10.3	5
1967 (l)	31.8	31.3	1
1968 (h)	61.3	25.0	2.5
1969 (l)	40.9	26.5	1.5

born in the second half of the year (Bujalska, 1975a; Gliwicz, 1975). Enhanced survival of the young of the spring generation in the years of high vole numbers may be related to better survival of their overwintered mothers (Bujalska, 1975a), especially since the age of overwintered animals is lower during high population numbers (Gliwicz, 1975). Differences in the survival of the youngest individuals, born in autumn, can be explained by changes in the pressure of older individuals on younger ones, which depends on the survival, and, consequently, on the number of individuals of the spring generation. As a result, in the years of low numbers, the survival of the young during the nesting period is considerably less variable than in the years of high numbers (Table 7.6).

The first breeding season (trappable individuals). As already noted, the group of independent individuals in their first summer is very heterogeneous. With respect to their mortality, this heterogeneity is most pronounced for mature and immature individuals, even if the animals of the same age are considered. Immature individuals survive much better than mature ones (Schwarz *et al.*, 1964; Bujalska, 1975a). Independent, trappable individuals which are not mature in the breeding season during which they were born usually belong to the autumn cohort. Schwarz *et al.* (1964) found an inverse relationship between the length of life and the intensity of growth, the rate of maturing, and the level of metabolism. In individuals of the spring generation, these processes proceed more rapidly than in individuals of the autumn generation, and are reflected in poorer survival of the former. According to Schwarz *et al.* (1964) the maximum length of life was 12 months for individuals of the spring generation and 14 months for those of the autumn generation. The period of increased

mortality (related to reaching maturity) occurred in the third and tenth months for these two groups, respectively.

Also Chitty & Phipps (1966) and Kaikusalo (1972) suggested that the independent individuals of the autumn cohort have a longer maximum life span and survive better than do those of the spring cohort. Smirnov (1972) additionally noted that in *C. rufocanus* and *C. rutilus* the highest survival in this period of life is characteristic of the autumn generation in the years of increasing population numbers.

Thus, the survival of trappable individuals in the year of their birth strongly depends on the time they were born, on their physiological condition, and on the phase in the population cycle. Interestingly in studies quoted above voles born in autumn suffer much heavier losses during the nesting period than do similarly-aged individuals in spring. They survive better and live longer if they pass this critical period and reach independence. It is not an infalable rule, however, since long-term materials obtained from the intense study of an island bank vole population in Poland show that the voles of the autumn generation do not survive better in the year of their birth than the voles of the spring generation (Gliwicz, 1976).

Winter season. All estimates of mortality in bank vole populations show that winter is a period of the lowest mortality, usually not exceeding 20% of the number of voles per month (Newson, 1963; Schwarz *et al.*, 1964; Bergstedt, 1965; Chitty & Phipps, 1966; Ashby, 1967; Gliwicz *et al.*, 1968; Smyth, 1968; Petruszewicz *et al.*, 1969; Smirnov, 1972; Bujalska, 1975a). This mortality is constant over the winter and equally affects different physiological and age classes. Some authors (Tanton, 1969; Kaikusalo, 1972) have recorded a drastic, short-term decrease in survival at the end of February and early in March. At that time mostly the voles in particularly poor condition die (mostly of the spring generation), mortality returns to the earlier, low level. The mean length of life for the bank vole is about three months. Winter (no reproduction) lasts for about six months. If the winter mortality equalled to the summer mortality, all individuals would die by spring.

Notably, a mortality decrease was also observed in species greatly differing from voles in their habits (hares, wild boars, and roe deer). The reasons for a low winter mortality usually include a generally older age structure of the population, a higher tolerance among the population members due to cessation of breeding, as well as lower mobility and intensity of contacts, reduced intra- and interspecific competition, and the reduced impact of predators under snow cover (Schwarz *et al.*, 1964; Smirnov, 1972). According to the literature data, factors determining winter mortality are snow cover (particularly in northern and eastern

Europe) and food availability. The duration of snow cover influences both the mean value of winter mortality and differences in mortality for various periods of winter if snowfalls are followed by sudden thaws and snow-free periods (Ilyenko & Zubchaninova, 1963; Schwarz *et al.*, 1964). The years of abundant acorn and beech mast are characterized by a particularly low winter mortality in the bank vole (Bergstedt, 1965; Hansson, 1971b; Bobek, 1973).

The second breeding season — overwintered animals. In contrast to the total agreement on characteristics of winter mortality, views on the fates of overwintered animals are not consistent. There is a general opinion that in early spring (April and early May) vole mortality is not much higher than in winter, and then it gradually increases. In mid-summer or in autumn, the last overwintered animals die (Newson, 1963; Chitty & Phipps, 1966; Ashby, 1967; Smyth, 1968; Gliwicz, 1975). The already noted differences in views focus on the composition of the overwintered groups. Some suggest that overwintered animals derive from the generation born in autumn, thus maturing in spring (Schwarz *et al.*, 1964; Smirnov, 1972). But in other populations the composition of overwintered animals varied greatly from year to year and this variation significantly modified the mortality of this group (Hansson, 1967a; Zejda, 1967; Gliwicz, 1975). For example, Gliwicz (1975) found that during years of high population numbers more than 50% of the overwintered animals were of the last autumn generation. But during years of low population numbers, more than 80% of the overwintered animals were recruited from the last spring generation. When the age structure of the population was younger, the overwintered animals survived much better than when the age structure was older. The direct cause of the differential mortality of the overwintered animals was not their age, since in the years of higher survival both the spring and the autumn generations survived better. Some intrapopulation factors must account for differences in survival from year to year. Apparently the survival of overwintered animals can be an important component of the regulatory mechanism in the bank vole population.

To summarize this section, it should be stated that factors determining mortality level can differ in each period of an individual's life. During the nesting period, the generally high and variable mortality can result from physiological and abiotic factors (thermoregulation, flood, ground frost), and also from intrapopulation factors, e. g., population density. In the first breeding season, the survival of independent individuals is mostly determined by their physiological status (whether they are mature or immature), which, in turn, depends on many intrapopulation and external factors. In winter, survival is critically linked

to environmental factors, and these factors do not fluctuate much, since winter mortality is very similar in various parts of the bank vole range. Conversely survival of overwintered animals can be heavily modified by intrapopulation factors. Because overwintered animals account for 100% of the population in early spring, changes in their mortality are of fundamental importance to population dynamics.

7.3.3. Other Factors Determining Survival

Annual changes in population mortality. When the data on the mortality are superimposed on general changes in the age structure of the population over the year, a pattern emerges of changes in mortality for an average population of the bank vole in the annual cycle. Though this is an average picture, it allows tracking in mortality against the background of population dynamics and changes in age structure (Fig. 7.9). In early spring (April) the survival of voles

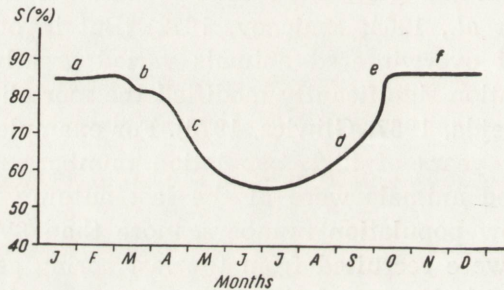


Fig. 7.9. Changes in survival for the whole population over the year. *a, f* — winter survival, *b* — early-spring decrease in the survival of overwintered animals, *c* — decrease in survival due to rejuvenation of the population age structure, *d* — increase in survival due to growing up of population members, *e* — sudden increase in survival after the breeding season, *S* (%) — survival index in per cent per month.

is very high as these are overwintered animals, which, as already noted, are characterized by a very high survival in the first half of the breeding season. Then their mortality increases and, at the same time, many young voles appear in the population, which are characterized by a low survival. Therefore, the poorest survival in an average population is in late spring and early summer. Afterwards (July-August), when most overwintered animals have already died and the population is composed of aging current-year individuals the survival increases. It should be remembered that the number of very young individuals, characterized by low survival, declines with the advance of the season, as the repro-

duction declines and the nesting mortality (of nontrappable individuals) increases. Consequently, the average mortality in the population should gradually decrease towards autumn, and then, as breeding declines, it should suddenly decrease to a minimum level that will be maintained, with small fluctuations, through winter.

Differentiation in mortality over the range of the species. The literature data on differences in the mortality of the bank vole in various parts of the range of this species are scarce. Generally, it seems that the maximum life span increases south-westwards. In southern Moravia, Czechoslovakia, Zejda recorded individuals that survived 21 months. Individuals living 18—20 months were recorded from Germany and southern Poland (Stein, 1956; Pucek *et al.*, 1968; Bobek, 1973). But the maximum recorded life span of bank voles from Scandinavia and Russia (central USSR) is 14—15 months (Ilyenko & Zubchaninova, 1963; Schwarz *et al.*, 1964; Bergstedt, 1965; Kaikusalo, 1972).

The permanency and depth of snow cover have the greatest effect on winter survival in northern and eastern areas of the range. In the populations inhabiting broad-leaved forests, autumn-winter mortality is clearly related to the abundance of food (most years), this relationship being absent in other habitats (Bergstedt, 1965; Bobek, 1969; Hansson, 1971a).

Mortality from predation. To explain some poorly understood events occurring in the population, it is frequently hypothesized that the impact of predators on the population varies. However, papers on the real impact of predators (reptiles, birds and mammals) on rodent populations in general, and on forest rodents in particular, are notably few. Southern (1959) and Southern & Lowe (1968) analysed relationships between population dynamics of the tawny owl, *Strix aluco*, the bank vole, and long-tailed field mouse, *Apodemus sylvaticus*. They found that during the breeding season, these rodents account for 70% of the vertebrate prey in the diet of the owl and that the predation rate on the bank vole is proportional to the density of these rodents. Goszczyński (1972), who studied the communities of forest rodents (*C. glareolus*, *A. flavicollis*, *A. agrarius*), field rodents (*Microtus arvalis*) and the whole community of predations (birds and mammals), found that in the years of average numbers of forest rodents predators remove up to 69% of their population, thus potentially they can control the number of rodents. But in the years of high population number (usually occurring in the same year for the bank vole and the common vole), the reduction of rodents by predators drops to 13%, thus the increasing populations presumably escape from control by predators. In forests, one of the most

important predators can be vipers (*Vipera berus* L.). It seems that among forest rodents they prefer the bank vole. The pressure of vipers is particularly high on the youngest animals on pregnant females, and on migrants (Pielowski, 1962; Pomianowska-Pilipiuk, 1974), thus in certain situations they can account for controlling numbers of the bank vole. Pearson (1966) has found that in open habitats (cropland, grassland, tundra), the 4-year population cycle observed in *Microtinae* rodents can be caused (directly and indirectly) by predators, while in forests such a regular cycle does not occur because of a much lower impact of predators on prey populations.

It should thus be stated that the effect of predators on population dynamics of the bank vole is still unknown. Even if it is not high in terms of numbers, it can be of great qualitative importance, particularly if the impact of predation increases during critical periods of the year for rodent populations, or if it affects selected age classes.