

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).

Laboratory and field studies provide many data on stimulating or inhibiting effects of abiotic and biotic environmental factors on reproduction. These factors modify successive stages of the breeding cycle, starting from the attainment of sexual maturity, through the development of a normal oestrous cycle and fertilization, to parturition and rearing the young. Each stage is sensitive to the effects of different factors. An ecologist is chiefly interested in the range of variability and actual values of particular components of reproduction in the population.

The methods used in field studies, and particularly the *CMR* technique, allow the application of only simple *in vivo* procedures of breeding condition assessment. Puberty of females is determined by observation of the perforation of the vaginal entrance. It usually is easily seen but sometimes a thin stick should be used to check the observation. Vaginal opening is almost always related to attainment of sexual maturity, though it happens that the first oestrus occurs later. Out of 42 cases of vaginal entrance opening occurred simultaneously in 33 cases; in one case it occurred after 8.5 days, and in seven remaining cases neither oestrous nor any other phase of the oestrous cycle was recorded over the observation period of 4.5 to 11.5 days (Bujalska, 1970). Therefore, the first oestrous should be considered as the unquestionable criterion of sexual maturity in females.

The phase of the oestrous cycle can be determined by analysis of vaginal smears. The method of taking vaginal smears is simple. Only a thin, cotton-tipped stick and a slide are needed. The material is stained and examined under a microscope. Bank vole cycles were monitored this way in the field by Larina & Golikova (1960), Bujalska & Ryszkowski (1966), Bujalska *et al.* (1968) and Bujalska (1970, 1973, 1975a, 1975b).

Distinguishing of pregnant females is possible by the analysis of vaginal smears (Bujalska & Ryszkowski, 1966; Bujalska, 1970) since absence of the oestrous cycle for longer suggests duration of pregnancy. Additionally vaginal smears of pregnant females may contain many erythrocytes (the exudation of blood from placenta), the mucus is smooth, unstructured, and frequented by leukocytes in 90% of pregnant females (Bujalska, 1970).

The presence of a copulation plug, and subsequent continuous increase in body weight 2—6 days before parturition are helpful (Bujalska, 1970). In *Clethrionomys rufocanus* 15-day pregnancy can be recognized visually (Kalela, 1957). When time extrapolation is possible, the most reliable sign of the past pregnancy is the presence of the young, or plucked fur around nipples.

The litter size can be determined *in vivo* only when parturition occurs in a trap, or in the nest if cannibalism can be excluded.

Also dead animals were examined, especially when the "Standard Minimum", the method recommended by the IBP, is used (Grodziński *et al.*, 1966). In this case the analysis involves the state of gonads in males and females, the uterus (the presence of embryos, their size and number, the occurrence of placental scars indicating past pregnancy). This kind of data is more exact.

Sometimes lack of direct data requires use of indirect indices e. g., of reproduction rate and recruitment rate, determining realized reproduction. For example, the analysis of the population age structure can be used to estimate the recruitment rate (Gliwicz, 1975).

As it is easy to rear bank voles under laboratory conditions (Drożdż, 1963; Buchalczyk, 1970), some information difficult to obtain in the field, particularly physiological parameters, can be assessed in captivity. Here are mostly involved estimates requiring series of observations, thus related to the trappability of animals, such as the duration of gestation period in relation to the litter size and the female, age, or the duration of the oestrous cycle and its phases. Ecological parameters, such as the attainment of puberty, number of pregnancies per female over the breeding season, and other parameters modified by the state of the population, should be measured each time in the population under study.

To calculate the number of newborn animals in a bank vole population, the formula described by Bujalska *et al.* (1968) may be used. It is a modified version of the formula used by Edmondson (1960):

$$v_r = \frac{\bar{N}_p TL}{t_p}$$

where v_r is the number of newborn over time T , \bar{N}_p is the average number of pregnant females, T is the study period in days, L is the litter size, and t_p is the gestation period in days. The value of \bar{N}_p allows the consideration of changes in the number of pregnant females, e. g. due to their mortality over the study period, but the calculated values of v_r is overestimated as compared with the real number of born, particularly when the number of pregnant females, N_p , increases. This is the case because of the assumption that a pregnant female gives birth to $1/t_p$ offspring every day, while in fact she gives birth to the whole litter at once, after t_p days. Therefore, if a female dies after time equal to $1/2 t_p$, one half of her litter size will be included into the number of born, while in fact zero individuals were born*. This error will be

* As a result of the overestimation of v_r , also the death rate of young voles from their birth to first capture is overestimated.

reduced when time T approaches t_p and the mortality of pregnant females is low.

The application of this formula in the studies on productivity (Bujalska *et al.*, 1968; Petruszewicz *et al.*, 1968) and demography of *C. glareolus* population (Bujalska, 1975a, 1975b) enabled calculating of nestling mortality, which is otherwise difficult to determine. The application of this formula is discussed in detail by Petruszewicz & Macfadyen (1970) and Petruszewicz (1978).

7.2.2. Age at Sexual Maturity

An important factor determining reproduction is the age at which the current-year animals reach sexual maturity. Usually females are considered here as they are directly responsible for population reproduction.

The number of mature females determines the potential reproduction of the population (Bujalska, 1970), and the percentage of mature females, together with the percentage of pregnant females, is an index of reproduction rate (Kalela, 1957).

Female bank voles become sexually mature at an age of 1–1.5 months, and males at an age of about 2 months (Buchalczyk, 1970). Field observations suggest, however, that even females less than one-month-old can be sexually mature. For example, 45-day-old females gave birth (Bujalska *et al.*, 1968).

The first information on the variable age of voles at sexual maturity is given by Kalela (1957). He noticed that the proportion of mature males and females in the population varied from year to year over three successive study years. In 1954 and 1956, when the population was low, almost all voles reached puberty in the year of their birth, the rate of maturing being slower in the second half of the breeding season, when the population size increased. In 1955, when the population was high, some females and almost all males failed to reach maturity in the current year. Where the population size was twice as high as in other places that year, neither females nor males reached sexual maturity in the year of their birth. These facts exclude the effect of meteorological factors on the rate of maturing. The only logical explanation could be the effect of population density.

A similar interpretation concerning the effect of population density on the age at sexual maturity in the bank vole was suggested by Zejda (1961, 1964, 1967) and Jewell (1966).

Koshkina (1965) attempted to explain ecological mechanisms responsible for changes in the rate of maturing of current-year individuals

at the beginning and at the end of the breeding season, as well as in different phases of the population cycle, on the basis of the studies conducted on a *C. rutilus* population in 1958—1964. This author relates the attainment of puberty to the actual population density and spatial requirements of mature individuals. Individual home ranges were larger at low- and smaller at high-population densities. Moreover, overlapping of home ranges increased with population density.

Therefore, the delay in reaching sexual maturity should be related to tendencies toward territoriality in mature voles. Territorial tendencies in mature females (in contrast to immature males and females) were also recorded by Naumov (1951) and Tanaka (1953) for *C. glareolus* and *C. rufocanus*. The relationship between the age at sexual maturity and the establishment of a territory implies that females can reach maturity at different ages and, critical for diagnostic purposes, at different body weights (Bujalska, 1970).

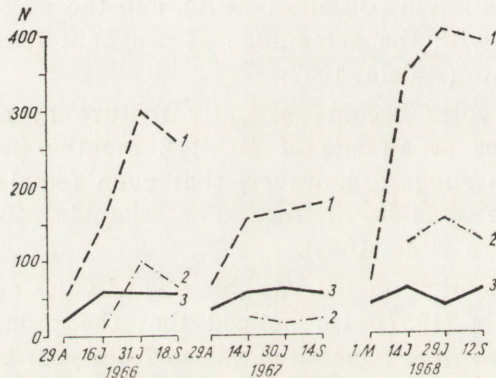


Fig. 7.3. Population size (1) and the number of immature (2) and mature females (3) of bank voles in different years. Dates of censuses on the x-axis.

These facts and their interpretation are consistent with a high stabilization of the number of mature females in an island population of the bank vole (Bujalska, 1970). In 1966—1968, the number of mature females was almost constant and independent of the population size (Fig. 7.3). This means that the number of females reaching maturity over the breeding season equaled the number of mature females that died in this time. The hypothesis of territorialism in adult females has been verified by such indices as (1) spatial distribution (mature females were evenly spaced, while immature females had a clumped or random distribution), (2) overlapping of individual home ranges (home ranges of neighbouring mature females only partly overlapped, while

those of immature females could overlap even three times), and (3) co-occurrence of females at particular trap sites: mature females were caught less frequently than randomly at the trap sites where more than one female occurred, while the trappability of immature females was independent of their number at a given trap site (Bujalska, 1970).

Then this hypothesis was experimentally tested when in June, 1969, about 50% of the females present in the population were removed. All of them were members of the first spring cohort (Bujalska, 1973). As the result, more females of the second and third cohorts reached maturity in July and September. In this way younger females "supplemented" the number of mature females to the level observed in earlier

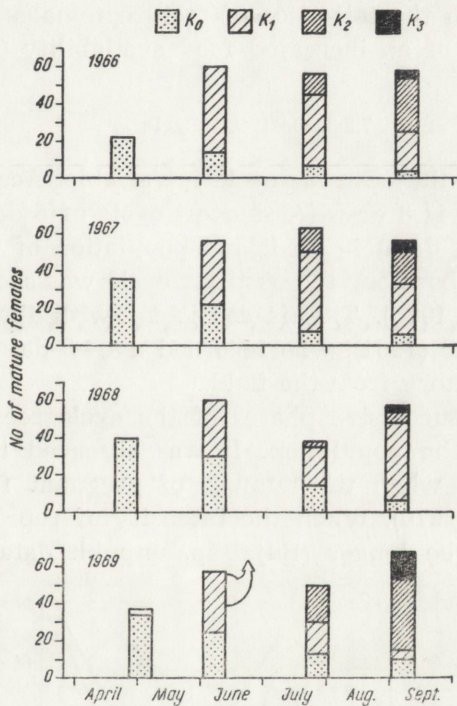


Fig. 7.4. Age structure of the mature female population. Arrow indicates number of voles removed.

years (Fig. 7.4). Differences in the age structure between mature females in September of 1966—1968 and of the year of the experiment show that younger females, born in the second half of the breeding season, are able to attain maturity in the year of their birth. This process, however, can be delayed because of the lack of "free" space they need to establish their territories.

It seems that tendencies toward territoriality in mature females are closely related to reproduction; after the breeding season both mature and immature females have random or clumped distribution (Bujalska, 1973). This suggests that the spacing of mature females, as expressed by the size of home ranges and the degree of their overlap, is related to the requirements of rearing young.

An experimental increase in food supply in the form of superabundant oast resulted in a decrease in the size of home ranges of all individuals, and this, in turn, was followed by an increase in the number of mature females (Bujalska, 1975a; Andrzejewski & Mazurkiewicz, 1976). No differences were recorded, however, in the type of spacing of the two female categories between the control and experimental years, though an increase in the tolerance of mature females could have been expected as a result of an increased food availability (Bujalska, 1975a).

7.2.3. Oestrous Cycle

Mean duration of the oestrous cycle is variable. According to Larina & Golikova (1960), it is 8 days. A shortest cycle of 5 days was observed by Bujalska (unpubl. data) in an island population of the bank vole in 1966—1968. In the laboratory the oestrous cycle was shorter and covered 4 days (Buchalczyk, 1970). This is consistent with the earlier data by Petrov & Ajrapetyanc (1961), who recorded a 4—5-day cycle in females brought to the laboratory from the field.

The duration of successive phases of the cycle seems to be related to the situation in the population. It was observed that the oestrous cycle was prolonged when the number of pregnant females increased (Fig. 7.5) (Bujalska, 1970). When the intensity of reproduction declined dioestrus tended to be longer (Bujalska, unpubl. data), and when the

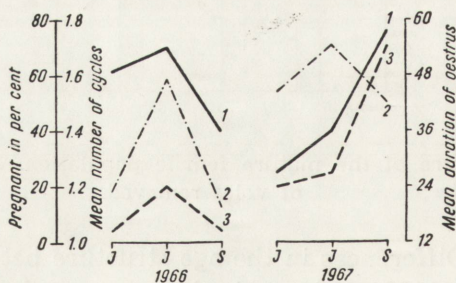


Fig. 7.5. Relation between percentage of pregnant females from cohort K_1 and variations in oestrous cycle.

1 — percentage of pregnant females, 2 — mean number of oestrous cycles per female during 14 days, 3 — mean duration of oestrous in hours. Dates of censuses on the x-axis.

population was overcrowded even all mature females stopped reproducing. In such cases symptoms of anoestrus (blocking the entrance to the vagina) occurred in females that reproduced 6 weeks earlier and resumed reproductions 6 weeks later, when the population declined (Bujalska, 1970).

According to unpublished data by Bujalska, in 1966—1968 proestrus lasted for 17.3 hours on the average, oestrus for 35.1 h, metoestrus 16.0 h, and dioestrus 56.3 h.

Post-partum oestrus can occur in the bank vole; at that time an effective copulation is possible as indicated by the occurrence of the vaginal plug immediately after parturition (Steven, 1957; Sviridenko, 1967). Post-partum oestri and vaginal plugs were frequently observed in an island population of the bank vole. In 1966—1968, the post-partum oestrus occurred 39.1 hours, on average, after parturition (Bujalska, unpubl. data).

Few data exist concerning the effect of exocrine factors (pheromones) on the oestrous cycle in small mammals in the wild. Such an effect is known for *Oryctolagus cuniculus* (Mykytowicz, 1965) and for various species living under experimental conditions (see Vanderbergh, 1973). An indication of a similar phenomenon in the bank vole is the fact observed by Larina and Golikova (1960) that females in the phase of proestrus leave their home ranges when there were no males around.

7.2.4. Duration of the Gestation Period

The gestation period of the bank vole found by different authors in various habitats varied from 17 to 30 days. For example, Wrangel (1940) reports 17.5 days, Popov (1960) 17—18 days, Bujalska & Ryszkowski (1966) 22 ± 2 days, and Naumov (1948) 20—30 days. Under laboratory conditions pregnancy usually covers 18—25 days (Drożdż, 1963), and the time span between successive parturitions is 20—57 days (Buchalczyk, 1970).

The interval of 16—35 days between successive litters under laboratory conditions (Table 7.2) implies that copulation occurred immediately after parturition or weaning. Intervals of about 2 months could be caused by the resorption of embryos or by the cannibalism of entire litters. Intervals of 4—9 months occurred in autumn and winter (Buchalczyk, 1970*).

* There are no conclusive data on the delayed implantation, thus a seeming elongation of the gestation period. For *Mus musculus* and *Rattus norvegicus* this was described by Baevski (1963). According to Wrangel (1940), the gestation period of lactating females rearing the earlier litter is 21.5 days. Mazák (1962) reports similar values (21—22.5 days).

Table 7.2.

Frequency distribution of time intervals between successive litters of the bank vole as expressed in numbers of females (n) and their percentage proportions (after Buchalczyk, 1970).

Time interval	n	%
16—35 days	212	45.6
to 2 months	82	17.6
to 3 months	65	13.8
4—5 months	72	15.3
6—9 months	33	7.0
9 months	1	0.2
Total	465	100

7.2.5. Litter Size

According to Zejda (1966), litter size varies from 5.24 in May to 4.4 in September (Table 7.3). Sviridenko (1967) found a similar range, namely from 4 to 5.6 young per litter. According to this author, litters are smaller in the wild, and they increase in the laboratory under optimum

Table 7.3.

Seasonal changes in the litter size of the bank vole expressed in the number of embryos. Number of litters in parentheses (after Zejda, 1966).

Months	Number of embryos
April	5.09±0.15 (55)
May	5.24±0.10 (147)
June	4.82±0.16 (67)
July	4.67±0.17 (42)
August	4.73±0.20 (30)
September	4.40±0.21 (20)

Table 7.4.

Geographic variability in litter size of bank voles. Number of litters in parentheses (after Zejda, 1966).

Location	Average litter size
Great Britain	3.95±0.08 (158)
Brittany	3.84±0.16 (43)
Czechoslovakia	4.90±0.07 (388)
North Germany	4.98±0.18 (57)
Kola Peninsula USSR	5.27±0.13 (102)
Moscow, USSR	5.53±0.15 (72)
Komi ASSR	5.47±0.22 (43)
Tatar ASSR	6.10±? (343)

conditions. Buchalczyk (1970) observed 1—10 young per litter in captivity (3.6 ± 1.46 on the average). 83.7% of the litters consisted of 2—5 young, and 3.3% were larger (7—10 young).

Zejda (1966) compared average litter sizes from different regions and he found that the litter size increased eastwards (Table 7.4). This may be related to climatic conditions.

The results obtained by Buchalczyk (1970) show that the litter size may be related to the age of females; females more than 15 months old delivered smaller litters than younger females.

Litter size can also be affected by resorption of embryos. For example, Coutts & Rowland (1969) observed a resorption of one or more embryos in 49—69% of pregnant females, and a resorption of more than 4 embryos in 5—6% of females.

7.2.6. Proportion of Breeding Females

The number of females taking part in reproduction of a population, e.g. the actual number of breeding females (Bujalska, 1970) varies considerably from season to season and from one year to another.

The proportion of pregnant females in the population examined by Sviridenko (1967) varied from 20—60% in different years. Bujalska & Ryszkowski (1966) have found that the proportion of pregnant females varied from 10 to 50% depending on the season, while Bujalska *et al.* (1968) found a 20—96% variation. Only in spring did the proportion of pregnant females approach 100% (Bujalska *et al.*, 1968; Bujalska, 1970).

Although there were differences in the number of pregnant females in an island population of bank voles, it has been found that the number of individual-days and, consequently, the number of voles born was stable in successive years (Bujalska, 1970, 1973). Removal of some individuals born in the year of the experiment (see section 7.2.2) resulted in an increase in the proportion of younger cohorts among mature females, and also accounted for the reproduction of females from the late-summer cohort (K_3). Females of this cohort did not reproduce in preceding years. This experiment confirms the earlier suggestions that recruitment of young cohorts to reproduction is of a compensatory character. As observations show, the percentage of pregnant females is always high for overwintered voles, while it varies greatly for the current-year cohorts (K_1 and K_2), always in an inverse proportion to the reproductive index of the overwintered females (Bujalska, 1970; Petruszewicz *et al.*, 1971). The percentage contribution of particular cohorts to reproduction in 1966—1968 as compared with that in 1969, when the removal experiment was carried out, is shown in Figure 7.4. Also Ryszkowski noticed that

the number of breeding females in different habitats in 1967—1969 was more stable than the total population size.

There are no empirical data explaining why reproduction is stabilized, or indicating ecological mechanisms underlying this stability. An experimental increase in the available food supply was not followed by an increase in the proportion of pregnant females (the number of pregnant females was a little higher, but also the number of mature females rose (Bujalska, 1975b).

7.2.7. Duration of the Breeding Season

In central Europe the breeding season of the bank vole extends from early April to late September. It may be locally shortened or prolonged. The beginning of the breeding season seems to be related to the time of snow melting and development of plant cover. For example, on Crab Apple island, in northwestern Poland, the onset of breeding was observed on April 1, March 25, March 30, and April 1, during 1966—1969, respectively (Bujalska, 1973).

The termination of breeding seems to be influenced by the population density. It lasts for a longer time at low population densities. For example, on Crab Apple island the breeding season of 1967, when the population was low, terminated with a delay of 10 days, that is, on October 10 (Bujalska, 1970). A similar relationship was observed by Zejda (1961) and Bergstedt (1965). Conversely, high population densities are coupled with a shortening of the breeding period (Zejda, 1961, 1964). The effect of climate, however, should not be neglected as the breeding season shortens northwards (Delany & Bishop, 1960).

Sometimes bank voles breed in winter. The reasons for this are not clearly understood. The results of Baker (1930) and Newson (1963) show that the winter breeding is not related to temperature. Zejda (1962) and Smyth (1966) suggest that food supply may be of some importance. This view has been supported by the results of a feeding experiment carried out in an island population of the bank vole. As a result of providing a superabundant oat supply the onset of breeding was accelerated by 6 weeks (Bujalska, 1975b), in effect, resulting in winter breeding (Andrzejewski, 1975). Also Watts (1970b) observed an earlier onset of breeding after enrichment of the habitat with food.

7.2.8. Recruitment of the Young

The realized reproduction, that is, the number of young becoming members of the trappable population depends not only on the birth rate, but also on the death rate during the nestling period, when the life

and development of the young depend on maternal care. This period seems to be particularly critical for both lactating females and nestlings. Lactation is a costly process in terms of energy (Kaczmarecki, 1966; see also section 8.1), therefore food deficiency severely affects lactating females and, consequently, their unweaned offspring.

Bujalska (1975a) found that the peak population of island bank voles was due to a decreased mortality of the voles of the spring generation, thus born shortly prior to the peak. Consequently, the average life span of this generation increased. The average length of life of the individuals of the autumn generation was much shorter, for example, in 1978, when the peak was high, the average life span of the spring and autumn generations (K_3 and K_4) was 128 and 53 days, respectively. In years lacking a high population peaks, the average length of life of the two generations was similar and much lower than that of the spring generation born before the peak. For example, in 1967 the average life of the two generations was 72 days. A positive relationship between the mortality of females rearing offspring and the mortality of the young of particular generations shows that all these changes were determined by nestlings survival (Bujalska, 1975a).

Further investigations (Bujalska, 1975b) showed that nestling mortality was related to food supply. When the population was provided with additional food in the form of oats, mortality of young of both spring and autumn generations declined. This implies that the survival of nestlings has a regulatory aspect.

7.2.9. Regulation of Reproduction

It may be concluded from studies on the bank vole that the reproduction of this species, as expressed by the potential and actual number of breeding females, varies less than mortality and, in particular, nestling mortality. Stabilization of reproduction in the island bank vole population followed the pattern shown in Figure 7.6.

The results obtained by Koshkina (1965) indicate that this pattern can also be valid for *C. rutilus* and, particularly important, for open populations of *Clethrionomys*.

A logical consequence of this pattern is that the main cause of changes in the population size of the bank vole may lie in mortality especially in nestling mortality. Bujalska (1977) suggested that changes in the size of the island bank vole population could be brought about in the way outlined in Figure 7.7.

In view of these findings some comments are needed on the concept of density-dependent regulation of reproduction. A stable or nearly stable

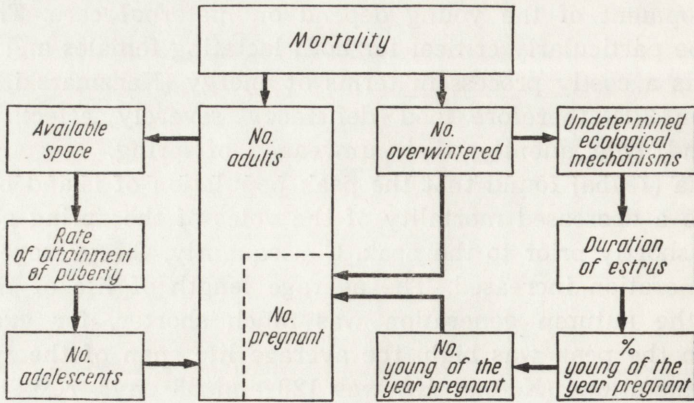


Fig. 7.6. Schematic representation of the processes stabilizing reproduction in an island population (after Bujalska, 1970).

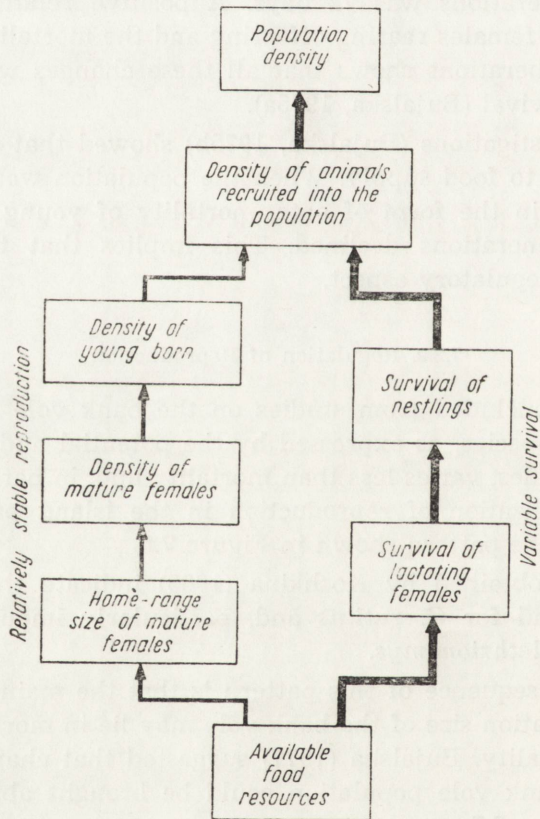


Fig. 7.7. A scheme of density regulation in a population of *Clethrionomys glareolus* (after Bujalska, 1977).

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