Poland, however, lies in the centre of the bank vole range, is small relative to the range of this species, and so is not likely to be a good place to follow such trends. Nevertheless, it has been found that bank voles from mountain populations in the Karkonosze Mts. are larger than those from Wrocław and submontane regions. These are, however, allometric relationships. The interpretation of this phenomenon should consider the degree of isolation of mountain forms as the bank voles inhabiting some peaks (e. g. Ślęża peak — 718 m above sea level, raising from a lowland) do not differ from those living in the lowland, and the voles inhabiting submontane areas have intermediate characters (Haitlinger, 1970).

Although the bank vole population from the Wrocław region is characterized by smaller body sizes than that from Białowieża, their subspecific position does not rises objections. Wasilewski (1952) classifies Polish bank voles to the nominative subspecies. In the same way, Haitlinger (1970) classifies the populations from the Carpathians and the Sudetes. Stein (1931) classifies voles from western Poland (Rybocice on the Oder river) to *C. g. glareolus* as well. Voles from south-eastern Poland were not classified to subspecies. Kowalski (1964) suggests that voles of the Kraków region may belong to the subspecies *C. g. istericus,* which includes the voles from western Ukraine (Tatarinov, 1956).

2.3. Individual Development

Marek GĘBCZYŃSKI

The period from onset of embryonic development to sexual maturity is called the period of individual development. From another point of view, individual development is considered as the whole individual life span, that is, it also includes the phase of maturity and aging. However, the sequence of changes in shape and functioning is most rapid until sexual maturity, therefore this period of life is of particular interest. In the bank vole it covers about 60 days, including 17—22 days of the embryonic (prenatal) development and then the postnatal development.

2.3.1. Embryonic Development

The gestation period in the bank vole varies from 17.5 days (Drożdż, 1963) to 18 days (Wrangel, 1940). In nursing females, it can be longer because the implantation of fertilized eggs is delayed (Brambell & Rowlands, 1936). Such a prolonged pregnancy usually lasts for 19—23 days (Drożdż, 1963; Buchalczyk, 1970), but sometimes up to 35 days (Buchalczyk, 1970). It may be assumed that the gestation period in the wild covers 22 days (Bujalska & Ryszkowski, 1966) (more information see section 7.2).

On day 3 after fertilization, the conceptus is divided into eight cells. Within 96 hours after fertilization, the blastocyst consists of about 50 cells (Mystowska, 1975), and it moves down the oviduct reaching

Table 2.2
Basic morphological characters used for aging embryos 15—18 days old (after Ożdżenski & Mystkowska, 1976b).

Character	Age of embryos (day of pregnancy)									
	9	10	11	12	13	14	15	16	17	18
Branchial arches	+	+	+							
Auditory vesicle	+	+								
Auditory vesicle, open			+	+	+	+				
Auditory vesicle, covered							+	+	+	+
Pigment in the eye			+	+	+	+	+	+	+	+
Eye-lid open				+[1]	+	+	+			
Eye-lid, closed								+	+	+
Physiological hernia				+	+	+	+[2]			
Vibrissae				+[3]	+	+	+			
Vibrissea protruding from the skin								+	+	+
Skin folds								+	+	+
Body weight mg		11	41	91	192	323	437	933	1056	1815
Crown-rump length, mm		4.5	7.0	9 5	11.0	12.5	14.5	19.5	20.0	26.5

[1] In some foetuses eye-lids are not yet developed, [2] Some foetuses are without hernia, [3] Visible in some foetuses only.

the uterus. Implantation takes place on day 5 of the development, when the blastocyst is elongated. After implantation the blastocyst grows rapidly, particularly in length. At the same time the polar trophoblast folds into the blastocoel. The allantoic cavity begins to develop on day 5 or 6, and during day 6 its particular parts join together to form a tube opened into the uterine lumen. The trophoblastic giant cells also develop on day 5 or 6, first from the peripheral trophoblast and later from the ectoplacental cone also. The number of these cells gradually increases so that they form a loose layer surrounding the embryo (Ożdżenski & Mystkowska, 1976a). In the bank vole also a phenomenon of the reversal of germ layers occurs. In the early stage of its formation, the embryo is, unlike the embryos of most mammals, semicircularly bent with its dorsal surface to the inside. Other rodent species show different degrees of the reversal of embryonic layers, and the bank vole belongs to highly specialized forms in this respect. It is not until the 9th day of development that the embryo assumes the shape characteristic of most mammalian embryos. Individual embryos can differ in the degree of their developmental advancement, but their characteristic features allow the determination of their age (Table 2.2).

Changes in the size and appearance of embryos, as well as changes observed in reproductive organs of the female allow the assessment of the stage of pregnancy during the post-implantation period; this is not possible earlier. On day 5 of gestation, implantation swellings are formed in the uterus. The gestation period can be dated by the size and appearance of embryos only between days 9 nad 15 (Ożdżenski & Mystkowska, 1976b). In the last three days of embryonic development, this aging estimation is not reliable because external morphological changes are small and the sizes of embryos are higly variable (Table 2.2). Prenatal development in size, weight and shape of bank voles as well as development of the skeleton show the same pattern of ontogenesis as do other altricial mammals (Sterba, 1976).

2.3.2. Morphological Changes in Postnatal Development

New-born bank voles are naked, blind, and virtually helpless. For the first dozen or so days of life they do not leave their nests, where the whole litter is attentively nursed by the mother. During that time their bodies become covered with fur, the eyes open, thermoregulation improves, and their diet changes. At the end of the third week, the young voles are sufficiently independent to leave the nest.

During postnatal development, young voles undergo a characteristic sequence of changes on consecutive days (Fig. 2.7).

One day of age. The skin of a newborn vole is naked and dark pink. Eyes are closed, but dark eyeballs are visible through the skin. The pinnae are not separated from the body, the acoustic meatuses are closed, toes are fused, and there are no teeth. The size (length in cm): body — 2.5—4.2; foot — 0.5—0.6; tail — 0.5—0.8.

Three days of age. No fur, but there is dark pigment in the dorsal skin. Upper parts of the tail and feet are grey. The size: body — 3.5—4.7; foot — 0.6—0.8; tail — 0.8—1.1.

Five days of age. The upper part of the body becomes dark and hair start to pigment (brown). The underside continues to be pink, with faint, whitish down. The incisors begin to erupt. The size: body — 3.7—4.8; foot — 0.7—1.0; tail — 0.8—1.2.

Seven days of age. Upper part of the head and the back are covered with short, dense, rusty grey fur; the venter is still pink but already covered with whitish hair. The pinnae are clearly separated, but the acoustic meatuses still closed. The toes partly separated. The upper and lower incisors are fully srupted. The size: body — 3.9—5.2; foot — 0.8—1.2; tail — 1.4—1.8.

Ten days of age. The body totally covered with short, dense pelage, rusty on the dorsal side and dark grey on the ventral side. Toes completely separated. The size: body — 4.8—6.0; foot — 1.0—1.3; tail — 1.8—2.2.

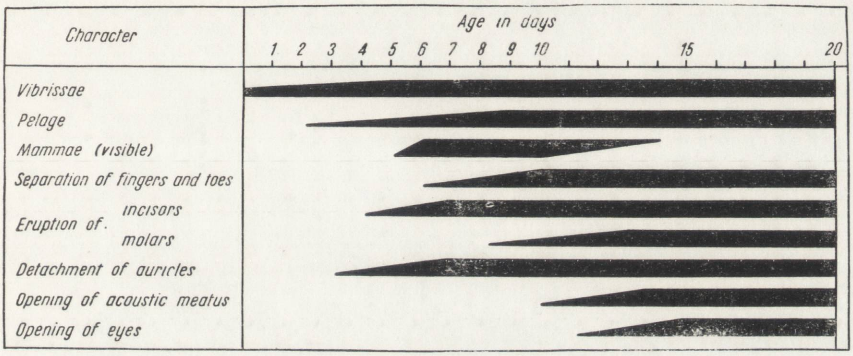

Fig. 2.7. Postnatal development of some morphological characters in the bank vole (after Sviridenko, 1959; Petrov & Ajrapetyanc, 1961; and Mazák, 1962).

12—13 days of age. The eyes are open and the animals respond to light. The acoustic meatuses are also open, and the response to sounds begins. Molars are protruding. The size: body — 5.4—6.2; foot — 1.2—1.4; tail — 1.9—2.2.

15 days of age. Fur coloration as in adults. Clear-cut response to vocal and visual stimuli. They run well and leave the nest for a short time. They begin to feed on solid food. The size: body — 5.3—7.1; foot — 1.5—1.6; tail — 2.2—3.3.

18 days of age. The teeth are completely developed, and the animals rely on themselves for food, though under laboratory conditions they sometimes continue to nurse. The size: body — 5.8—7.8; foot — 1.5—1.7; tail — 2.7—3.4.

20 days of age. The size: body — 7.7—8.0; foot — 1.6—1.7; tail — 2.8—3.5.

26 days of age. The size: body — 6.9—8.0; foot — 1.6—1.7; tail — 2.8—3.6.

30 days of age. The size: body — 7.3—8.4; foot — 1.6—1.7; tail — 3.0—3.6.

35—40 days of age. The size: body — 7.6—8.7; foot — 1.7—1.8; tail — 3.4—4.2.

2.3.2. Growth Rate

Body weight of bank voles in their first month increases rapidly, being a little less than 2 g at birth (Sviridenko, 1959; Mazák, 1962; Zejda 1968; Ożdżeński & Mystkowska, 1976b) and 11—15 g (Fig. 2.8)

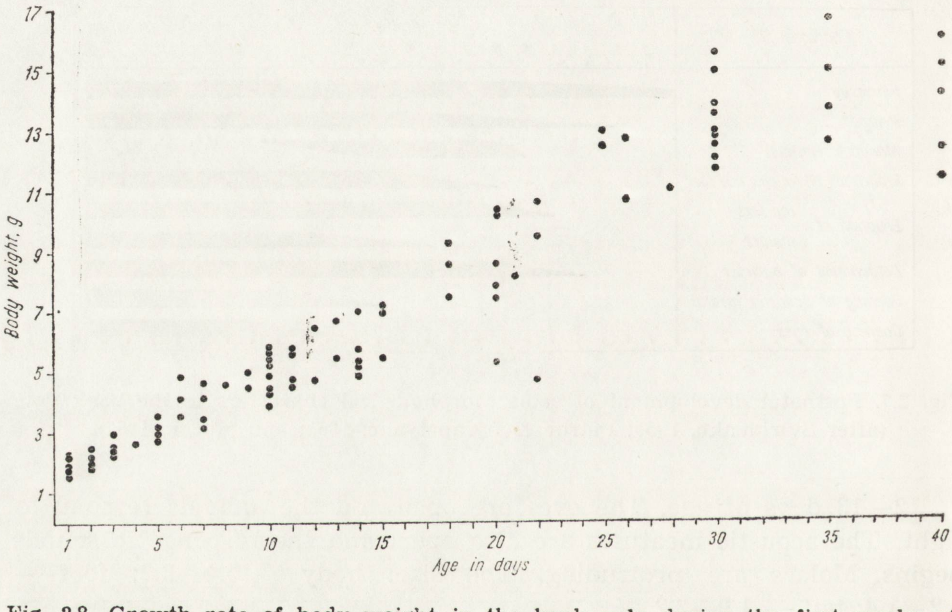

Fig. 2.8. Growth rate of body weight in the bank vole during the first weeks of life (after Sviridenko, 1959; Petrov & Ajrapetyanc, 1961; Mazák, 1962; Pearson, 1962; Drożdż, 1965; Bujalska & Gliwicz, 1968; Fedyk, 1974a, 1974b, Sawicka-Kapusta, 1974).

at the age of 30 days (Mazák, 1962; Drożdż, 1965; Bujalska & Gliwicz, 1968; Fedyk, 1974a, 1974b; Sawicka-Kapusta, 1974).

It is not known whether under natural conditions the growth of bank voles in their first month depends on the season. Although the season has an effect on the rate of the development of physiological maturity, it seems that there are no significant differences in the growth rate between spring and summer generations. Under experimental conditions, a decrease in the costs of rearing offspring in terms of energy is due to a decrease in their growth rate (Gębczyński, 1975). Under natural conditions, however, the same effect may be reached by a decrease in the litter size. The latter view is conistent with the fact that in autumn the litter size is smaller than in spring by 40% (Zejda, 1966; Ryszkowski & Truszkowski, 1970). It may thus be expected that the growth rate during nesting development is similar, independent of the season at birth. It is possible that an individual of small body size would have little chance for survival after weaning.

It is well known, however, that the further growth, when the animals are two and three months old, is more rapid for the spring cohort as compared with the autumn one (Wasilewski, 1952; Ilyenko & Zubchaninova, 1963; Bergstedt, 1965; Kubik, 1965). Experimental evidence shows that both poor food conditions (Sviridenko, 1959) and low ambient temperature (Gębczyński, 1975) can inhibit the growth of young voles. Nonetheless, it is suggested that under natural conditions the growth rate of the bank vole is stable over the first 3—4 weeks, independent of the season (Bujalska & Gliwicz, 1968; Zejda, 1971; Fedyk, 1974b; Sawicka-Kapusta, 1974). A different view is presented by Bergstedt (1965). It should be emphasized, however, that all the statements on the rate of growth in the nest are in fact based on laboratory data, or they are extrapolations from values for the voles caught in their second month. How difficult it is to determine the age of growing voles under natural conditions may be indicated by the fact that according to Bergstedt (1965) ten-day-old bank voles can leave their nest for a short time. Existing data on postnatal development, however, document that at this age they are still blind.

The body weight of 20-day-old bank voles from litters of 3—5 young is higher than those from litters of 6—9 (Korabelnikov, 1972). But the litter size dose not seem to have an unequivocal effect on growth rate. Vetulani (1931) discovered that mice kept singly grew less rapidly than those kept together. Moreover, as indicated above, the rate of growth depends markedly on many other factors, therefore it cannot be related to the litter size in a simple way. The data collected by Pearson (1962) and Mazak (1962) reveal that 10 to 12-day-old bank voles grow more slowly than do older animals. Many other data (Bujalska & Gliwicz, 1968; Fedyk, 1974a, 1974b; Sawicka-Kapusta, 1974) show that the growth rate is variable over the first 40 days, but it is not possible to distinguish fixed periods of faster and slower growth. Observations of many litters seem to suggest rather that growth rate depends on the varying ability of females to nourish their offspring.

2.3.4. Physiological Development

New-born bank voles are physiologically immature, and different functions develop on consecutive days after birth. Only some of them have been thoroughly studied. They include morphological parameters of blood that determine the respiratory function of this tissue. The highest hemoglobin level (20g %) occurs immediately after birth. Then it rapidly decreases to a minimum of 13 g% on days 6—7. In older voles it elevates to about 16 g% at the age of 30 days (Kostelecka-Myrcha, 1967). Similarly, clear-cut changes were observed in the number of erythrocytes and in the hematocrit index (Table 2.3). The rate of oxygen

Table 2.3.
Age-related variability of some blood indices in the bank vole (after Kostelecka-Myrcha, 1967).

Index	Age in days			
	0—1	4—6	30—32	68—70
Haemoglobin, g%	20.0	13.0	16.0	16.7
Number of erythrocytes, $\times 10^6$	5.33	4.12	10.93	11.52
Haematocrit, %	49.6	32.3	46.3	45.9

Table 2.4.
Rate of oxygen intake (μl/dry mg·hr) by homogenized heart and kidney during postnatal development of the bank vole (after Gębczyński, 1976).

	Age in days				
	1—3	10—12	19—21	28—30	31—45
Heart	4.48	4.47	4.08	3.86	3.64
Kidney	2.96	2.79	2.92	2.42	2.15

consumption by homogenized heart and kidney varied with age, but there were differences between the two organs (Table 2.4). Another interesting feature observed in some rodent species, including the bank vole, is the ability to utter ultrasounds at low ambient temperatures (Okon, 1972). This may be interpreted as a means of communication between the young and the mother when their body temperature drops and they want her to return to the nest to warm them. This suggestion concurs with the fact that the ability to produce ultrasounds disappears when their thermoregulatory system is well developed.

The rate of physiological development also depends on the season in which the young are born. Bank voles born in spring are characterized by more mature body composition (as expressed by the protein to water ratio) than those born in autumn (Fedyk, 1974b). This implies that the autumn generation is physiologically younger than the spring one.

Similar measurements of tissue metabolism indicate that the autumn generation is physiologically younger than the spring generation of the same absolute age, and that this generation develops at a lower rate (Gębczyński, 1977).

The development of homeothermy. A specific physiological feature of postnatal development is the increasing ability to maintain a stable body temperature. It depends on the formation of mechanisms of heat production (chemical thermoregulation), ability to control heat losses (physical thermoregulation), and the development of the temperature regulation centres.

Table 2.5

Age-related changes in oxygen intake (ccm/g·hr) in bank vole litters at different ambient temperatures (calculated from data by Gębczyński, 1975)

Litter size	1—9	10—18	19—33
	Age in days		
	Ambient temperature 15°C		
1—2	3.96	4.70	4.54
3—6	3.04	3.97	3.73
	Ambient temperature 20°C		
1—2	2.09	3.87	3.50
3—6	2.13	3.24	3.45
	Ambient temperature 25°C		
1—2	4.20	3.38	2.96
3—6	1.85	2.75	3.12
	Ambient temperature 30°C		
1—2	3.26	2.66	2.72
3—6	1.60	2.54	2.82
	Ambient temperature 35°C		
1—2	2.38	3.00	3.05
3—6	1.38	2.93	3.22

The rate of heat production in the bank vole increases with age (Bashenina & Borovskaja, 1963), but it also largely depends on the litter size (Gębczyński, 1975). Young bank voles from small litters (1—2 individuals) differ in their metabolic level from those raised in larger litters (3—6 individuals). These data (Table 2.5) clearly show that bank voles are able to increase their heat production in response to low temperatures already in the first days of life. This metabolic reaction is certainly not sufficient to maintain a stable body temperature for a longer period as both the energy reserves of a young organism are small and the loss of heat is relatively rapid. The rate of heat loss gradually diminishes during the first ten days as the bodies of originally naked animals become covered with the fur (Sviridenko, 1959; Mazák, 1962). It should be added that pelage development is accomplished at an age of 19—20 days, coinciding with a complete development of thermoregulation. The body temperature of young bank voles during their first nine days is about 4.5°C lower than that of adults. It undergoes only small changes, though the ambient temperature varies greatly (Fig. 2.9). The body temperature of 10—18-day-old bank voles increases daily, and reaches the adult body temperature on day 19.

Factors compensating for the lack of efficient thermoregulation in young voles involve an extensive parental care (*e. g.* complicated nest structure in close relation to ambient temperature and by attending the

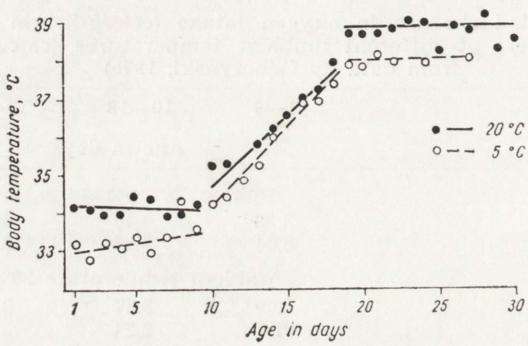

Fig. 2.9. Body temperature of the bank vole in relation to age and thermal conditions (after Gębczyński, 1975).

young for most of the day). Another important factor is the huddling behaviour of the young. They form a densely packed group responding as a unit to thermal cues during the nesting development (Gębczyński, 1975). All these factors account for relatively stable living conditions in the nest, which may be necessary for normal growth and development of the bank vole.

B i o e n e r g e t i c s   o f   g r o w t h. The cost of maintenance of well protected bank voles permanently staying in their nests is small. It may be expected, therefore, that their rapid growth is an energetically efficient process. An index of this efficiency can be the ratio of the energy stored in the body to the energy assimilated from food. The assimilated energy (A) is used for costs of maintenance (R = respiration) and it can also be stored in the form of body components (P = production). From these two values, the coefficient of production efficiency can be calculated as follows:

$$K = P/A \cdot 100$$

The amount of energy stored in the body tissues (P) of a growing organism can be precisely measured as it is equal to the product of the body weight and its energy content per unit weight. The energy content of the body varies markedly during the first few weeks of life. Although the energy content of fat and proteins is constant and independent of age (Fedyk, 1974a), the relative water content drops with age. A six-fold increase in the content of water is coupled with a four-fold increase in the content of protein and a 50-fold increase in the content of fat (Fedyk, 1974b).

It has been calculated (Gębczyński, 1975) that during the first nine days of life (when the young do not leave their nest, their metabolism being relatively low and the rate of growth not lower than later, 60% of the assimilated energy is allocated for production (Table 2.6).

In 10-18-day-old voles the efficiency of production is significantly reduced, but still high. In older *C. glareolus* it does not exceed 5%

Table 2.6

Energy requirements and growth efficiency in bank vole litters consisting of four individuals in successive periods of postnatal development (after Gębczyński, 1975). $K=P/A\cdot100$ and $A=P+R$; K denotes the coefficient of production efficiency, P is tissue production (weight increase), R is respiration (maintainence costs), and A is assimilation (sums production and respiration)

Age in days	Mean litter wt., g	Oxygen intake ccm/g·hr		kcal/litter per day	Effeciency K, %	
		at 30°C [1]	at 35°C [1]		1 [2]	2 [3]
1—2	12.4	1.51	1.30	1.98	59.5	46.5
10—18	25.2	2.27	3.02	8.22	19.3	9.4
19—33	44.0	2.90	3.31	33.87	—	4.5

[1] It has been assumed that the female is outside the nest for about six hours a day, and the nest temperature in this time is 30°C. It has also been assumed that when the female is in the nest, the temperature for the young is about 35°C. To simplify the calculations, it has been assumed that the group of the oldest bank voles live in the same ambient temperature as younger individuals do, though the former remain in the nest only for some part of the day.

[2] Changes in the body composition after data by Sawicka-Kapusta (1974)

[3] Changes in the body composition from data of Fedyk (1974b).

(see also section 8), and it is equal to that of *Microtus arvalis* (Drożdż *et al.*, 1972).

Thus, bioenergetic parameters of the bank vole undoubtedly undergo substantial changes within a short time after birth. The efficiency of tissue production is very high until homeothermy is eventually developed. The cost of tissue production are highest for individuals with completely developed thermoregulation.

The developmental stage at birth can influence the differentation of the rate of growth and physiological maturation during ontogeny. The period of growth *in utero* and during postnatal development are complementary. This plasticity in reproduction, enabling adult bank voles to shift their care from the prenatal to the postnatal period, is a sign of a high evolutionary adaptability of this species. The shift is, perhaps one of the mechanisms which enabled the bank vole to spread over many different Eurasian habitats. This pattern of individual development largely alleviated the energy problems related to small body sizes (at the expense of temporary vulnerability) not only for the bank vole but also for many other small mammals.