

Life history of voles: growth and maturation in seasonal cohorts of the root vole

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Gliwicz, J. Life history of voles: growth and maturation in seasonal cohorts of the root vole. *Misc. Zool.*, 19.1: 1-12.

Life history of voles: growth and maturation in seasonal cohorts of the root vole.— Seasonal differences in growth and maturation patterns in voles can be direct effects of changing environmental factors or indirect, evolutionary selected responses to environmental signals. The aim of the study is to examine growth and maturation in seasonal cohorts of wild populations of the root vole, *Microtus oeconomus*, and to investigate causes for stated differences in the patterns. Three cohorts of young of the year (K1-K3) and one of overwintered old individuals (K0) were distinguished. Young born in different seasons differed in continuity of growth throughout the breeding season and in maturity. The first signs of the seasonal inhibition of growth and maturation in subadult summer born voles (K2) were found before mid-July. The inhibition is interpreted as an adaptive response which increases chances of these individuals to survive the winter. The possible environmental cue to which they respond, and the possible advantages of refraining from further growth are discussed. Existing models of optimal energy allocation to growth and reproduction, which do not fit small rodents, appear to be inadequate.

Key words: Growth, Life history, Maturation, *Microtus oeconomus*, Seasonal cohorts.

(*Rebut: 15 XI 95; Acceptació definitiva: 2 I 96*)

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This work was supported by grant no. R/05/033/90-2 of Ministry of National Education, and by grant no. 411789101 of the Committee for Scientific Research.

Introduction

Small rodents such as biannual, polyestrous mammals provide an interesting case for life-history studies. Differences in patterns of growth and reproduction related to the season of birth has been reported for many mouse and vole species living in seasonal environments. This aspect has been most fully studied in microtine rodents.

The main differences occur between spring and autumn cohorts: spring born young grow fast, mature early and breed in the year of birth, whereas those born late in the reproductive season grow slowly, remain immature and do not reproduce until the following season (BARBEHENN, 1955 for *Microtus pennsylvanicus*; SCHWARTZ et al., 1964 for several *Microtus* species; REICHSTEIN, 1964 for *M. arvalis*; GLIWICZ et al., 1968 for *Clethrionomys glareolus*; PINTER 1968 for *M. montanus*). In several other studies three seasonal cohorts were distinguished, with summer individuals having intermediate characteristics between those of spring and autumn cohorts (ZEJDA, 1971 for *C. glareolus*; MARTINET & SPITZ, 1971 for *M. arvalis*; MYLLYMAKI, 1977 for *M. agrestis*).

In general, there are two theoretical approaches to the causes of inhibition of growth and maturation in voles born later in the season. According to some authors, the external factors which vary seasonally, directly affect growth and maturation of voles. Lower temperature (PEARSON, 1962), shorter day (BASHENINA, 1960), inferior food quality (BERGER et al., 1981) or the combination of these factors, e.g. temperature and photoperiod (REICHSTEIN, 1964), food and photoperiod (PINTER, 1968; MARTINET & SPITZ, 1971) were most often indicated as factors slowing down growth and/or delaying maturation. As a result, voles born later in the season grow and develop so slowly that they are unable to mature before the beginning of winter. Other authors, however look at this phenomenon as an evolutionary selected strategy of later born individuals. Repro-

duction is postponed for the next season in order to maximize their chances of surviving winter and to increase their future reproductive output (for review, see COCKBURN, 1988). In this case, the most important seasonal difference for early-born and late-born young would be 'time-to-go' i.e. time left to the end of the breeding season (KOZŁOWSKI, 1992). Seasonally changing conditions should affect voles only indirectly, acting as «warning signals» of approaching winter, and the rodents would physiologically adjust their growth and reproduction accordingly.

Results of the few studies in which three seasonal cohorts were examined indicate that the first signs of inhibition of maturation occur in summer, when environmental conditions are still mild. This supports the second hypothesis, suggesting adaptive switching of later born voles, and encouraging further investigation of this process.

The aim of this paper is to distinguish between direct and indirect effects of seasonally changing environmental factors on development of young voles. For this purpose, growth and maturation of three seasonal cohorts of young root voles, *Microtus oeconomus* living under field conditions were examined in detail, with special attention paid to the summer period, when first signs of growth and maturation inhibition were expected.

Material and Methods

The population under study inhabits a small peninsula of Lake Ros near Pisz (53° 36'N, 21° 25'E) in the Mazurian Lake District. The peninsula, about 4 ha in area, is covered by humid meadows composed mainly of *Carex fusca*, *C. rostrata* and *Poa palustris*, and in part by alderwood. The meadows are partly overgrown by willow shrubs (*Salix pentandra* and *S. cinerea*), typical for early stage of succession towards Salici-Franguletum association.

Material was collected from July 1989 to September 1991. The population was

followed by live trapping and snap trapping. Live trapping was performed on ca. 1 ha grid situated in the meadow. Snap traps were set in other parts of the meadow, more than 100 m from the grid, and in alderwood.

Trapping sessions were performed at regular intervals five times during each trapping season from April to September, average days of trapping being: 20 April, 5 June, 15 July, 10 August and 10 September.

The main source of material came from dead animals caught in snap traps (some voles were previously marked on the live trap grid), those found dead in live traps and some purposely removed from the trapping grid for age estimation. In addition to regular sessions, one winter snap trapping was performed in February, but only seven voles were caught. A total of 257 individuals were dissected and used for the analysis.

Data from live trap grid on which voles were individually marked, weighed at each capture, sexed and observed for signs of sexual maturity, pregnancy and lactation, provided additional information about the individual and population characteristics. In 1989 and 1990 the population density was higher (over 100 individuals per ha at maximum) than in 1991 (max. 26 individuals per ha), but regular population cycles have not been reported for this species in Poland.

All dead animals were weighed and eyeballs were removed. In dissected males the position of testes was noted and their length and width were measured. In females uterus was checked for signs of previous pregnancies and presence of embryos. In pregnant females, the weight of the uterus with embryos was subtracted from the body weight, and these corrected body masses were used for further analysis.

The eyeballs were processed according to a standard method used for age estimation (e.g. HAGEN et al., 1980). The weight of both lenses was used as the reliable indicator of relative age in the voles, since

it could be referred to the absolute age (expressed in months) only for younger individuals (up to three months of age). As of this age the curves relating lens weight to absolute age, given by different authors for various geographical populations, diverge (HAGEN et al., 1980; MARKOWSKI, 1980). For this reason, age is expressed as eye lens weight.

Results

Cohorts distinguished

Young born during each breeding season were divided into three cohorts on the basis of their first appearance in the traps:

K1. The spring cohort was composed of individuals trapped for the first time in late April. Their age estimated on the basis of average lens weight (table 1) was about one month (HAGEN et al., 1980; MARKOWSKI, 1980). This indicated that they were born on average on March 20, and that the breeding season began about March 1 (the gestation period for the root vole being 20-21 days, TAST, 1966). These young were born by overwintered voles.

K2. The summer cohort consisted of young that became independent during June and the first weeks of July. They were offspring of overwintered and K1 individuals.

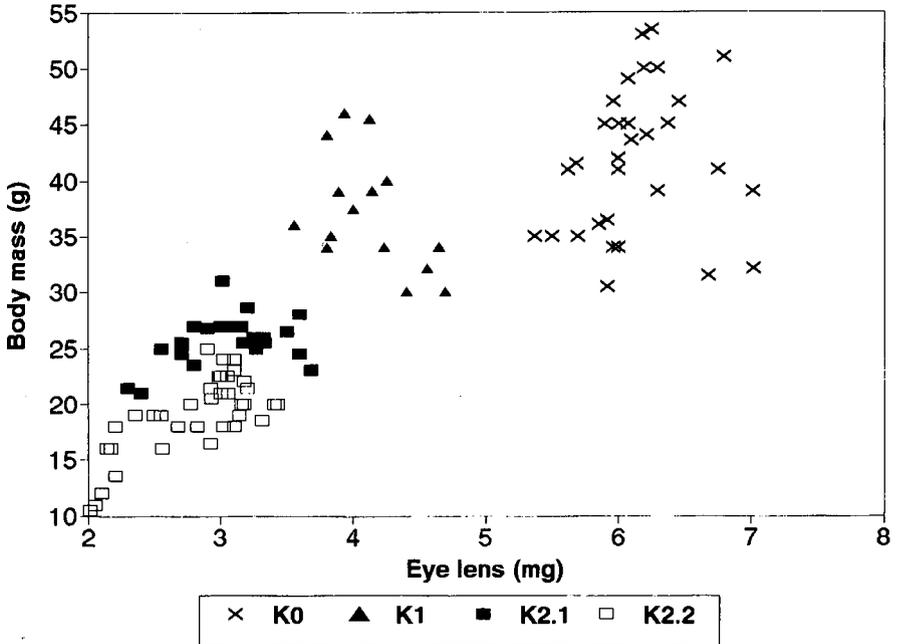
K3. The autumn generation was formed by individuals which left nests between the end of July and the end of the breeding season. The last trapping session of the year, carried out between 5-15 September, indicated that by this time the breeding season was over. Testes of males were in the seasonal regression, no female was pregnant and very few (< 10%) were still lactating.

In addition to cohorts of the year, the overwintered cohort (K0) was identified. Throughout the study these old voles were present in the population till mid-July, after which they rapidly died off.

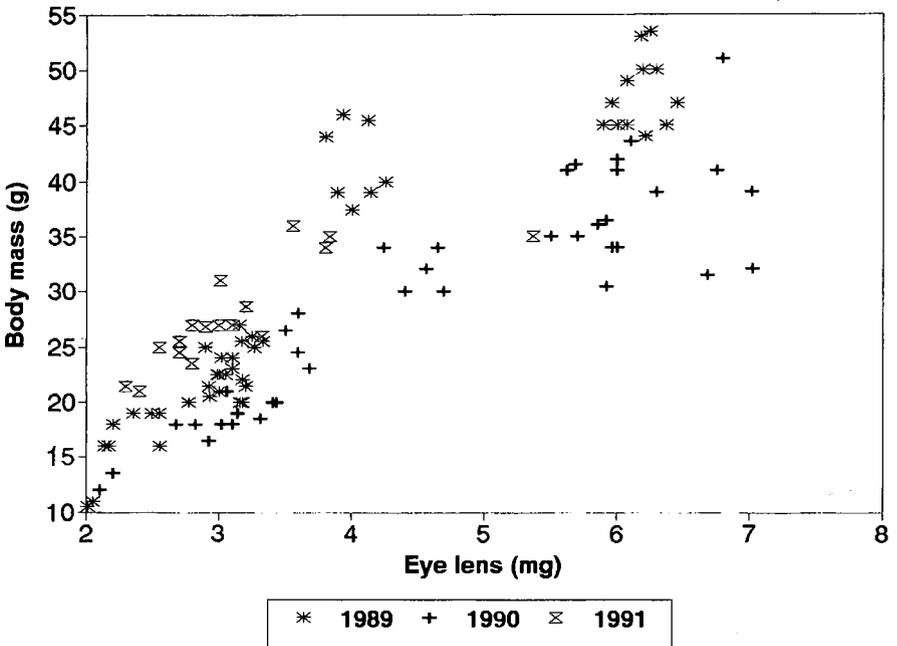
Table 1. Eye lens weight and body mass (mean \pm S.E.) of different seasonal cohorts of the root vole. (Numbers in brackets indicate sample size used for body mass estimation). ^{abcdef}. Mean body masses with the same superscript differ significantly within the cohorts of individuals of the same age.

Peso del cristalino y del cuerpo (media \pm D.E.) de distintas cohortes estacionales del topillo nórdico. (Números entre paréntesis indican el tamaño muestral utilizado para la estimación del peso corporal). ^{abcdef}. Masas corporales con el mismo superíndice difieren dentro de las cohortes de la misma edad.

Cohort	n	Eye lens (mg)	Body mass (g)	Unpaired t-test
20 April				
K0 ♂	10	5.54 \pm 0.14	33.9 \pm 1.97 ^a	lens ns; body: t = 2.24 df = 20, P < .05
K0 ♀	12	5.24 \pm 0.09	28.5 \pm 1.50 ^a	
K1	7(14)	2.42 \pm 0.05	24.2 \pm 1.10	
5 June				
K0 ♂	8	5.80 \pm 0.11	42.5 \pm 1.96 ^b	lens ns; body: t = 4.53 df = 19, P < .001
K0 ♀	13	5.58 \pm 0.08	30.5 \pm 1.74 ^b	
K1	11	3.01 \pm 0.08	30.1 \pm 0.51	
K2	17(25)	2.16 \pm 0.07	14.9 \pm 1.18	
15 July				
K0 ♂	7	6.28 \pm 0.13	42.6 \pm 1.84 ^c	lens ns; body: t = 3.66 df = 16, P < .05
K0 ♀	11	6.08 \pm 0.09	35.1 \pm 1.14 ^c	
K1	15	4.13 \pm 0.10	36.5 \pm 1.33	
K2.1	21	3.12 \pm 0.11	25.3 \pm 0.54 ^d	lens ns; body: t = 8.48 df = 50, P < .001
K2.2	31	2.88 \pm 0.06	19.7 \pm 0.41 ^d	
10 August				
K1	9	4.59 \pm 0.10	37.0 \pm 1.70	
K2.1	12	3.37 \pm 0.05	26.4 \pm 0.96 ^e	lens ns; body: t = 5.74 df = 24, P < .001
K2.2	14	3.52 \pm 0.17	20.2 \pm 0.58 ^e	
K3	17	2.50 \pm 0.20	15.6 \pm 1.04	
15 September				
K2.1	9	4.17 \pm 0.06	26.8 \pm 0.73 ^f	lens ns; body: t = 6.25 df = 17, P < .001
K2.2	10	4.08 \pm 0.06	20.9 \pm 0.61 ^f	
K3	11	2.98 \pm 0.09	17.3 \pm 0.30	
Winter				
K0 ♂	4	5.09 \pm 0.12	4.3 \pm 0.67	
K0 ♀	3		21.0 \pm 0.99	



A



B

Fig. 1. Differentiation of individuals in mid-July. A. Cohorts distinguished (mature individuals of K2 - black rectangles); B. data from different years.
Diferenciación de individuos a mediados de julio. A. Cohortes diferenciadas (individuos maduros de K2- rectángulo negro); B. Datos de distintos años.

Body weights in relation to lens weights of all individuals dissected in July showed three distinct groups -cohorts K0-K2 (fig. 1a); the pattern was consistent from year to year (fig. 1b). The July sample has been chosen for illustration because at that time of the season the population was most differentiated with respect to age and reproductive status of individuals. The proportion of individuals in each group in figure 1 shows the age composition found in the live trapped population in July.

The first group was composed of the oldest individuals with lens weight above 5 mg. These were overwintered voles (K0). There was a high variation in the lens mass, and even higher in the body mass of this group. This variation in body weight may be attributed to between-year differences (fig. 1b). K0 individuals in 1989 were significantly heavier than those in 1990-1991 (unpaired t-test, $t = 6.87$, $df = 16$, $p < 0.001$ for females and $t = 2.82$, $df = 10$, $p < 0.01$ for males), though not older (eye lenses did not differ significantly; one-way ANOVA for years and sexes $F = 1.58$, $df = 28$, $p = 0.22$).

The next distinct group was formed by individuals with lens weight 3.7 - 4.7 mg, and relatively high (> 30 g) body mass (fig. 1). These were K1 individuals. The narrow range of their lens masses each year (fig. 1b) indicated the synchrony in their birth early in the spring. In July all K1 individuals were sexually matured, and all dissected females were pregnant or lactating.

The third group consisted of individuals with eye lens weighting less than 3.75 mg, and body mass distinctly lower than in the K1 group. They belonged to the summer cohort, K2 (fig. 1b).

K2 individuals in July were strongly differentiated in their reproductive status. Some of them were matured, even pregnant, whereas others did not show any signs of maturation. Observations of live trapped individuals revealed that those young which did not mature in July, remained immature for the rest of the breeding season.

Growth characteristics

For each cohort, season, year and sex (in K0 and K1), mean body weight and lens weight were calculated and tested for statistical differences among years, between sexes and between mature and immature individuals of K2 cohort (table 1). It was found that data for all years (1989-1991) could be pooled (with the above mentioned exception of significantly heavier K0 in 1989, excluded from further analysis). Sexual dimorphism in the body mass was apparent only in the overwintered cohort (table 1). Among the summer-born individuals (K2), body weights of mature (K2.1) and immature (K2.2) voles became statistically different in July, and the difference continued to the end of the season (table 1). The winter sample was too small for statistical analysis.

Mean values presented in table 1 were used for construction of growth curves for different cohorts (fig. 2). The first point on the plot is based on the mean value obtained for the youngest individuals ($n = 9$) caught throughout the study period, regardless of the season. Their body weight ranged from 9-11 g, and lens weight 1.6-2.0 mg. Their age was estimated as less than 20 days, indicating they were just weaned (TAST, 1966; GEBZYNSKA & BUCHALCZYK, 1969; HAGEN ET AL., 1980). This data point was assumed to be common for individuals of all cohorts. For the overwintered cohort in which lens masses of females and males, unlike their body masses, did not differ significantly, average lens weights were used for plotting.

There were two periods of fast growth of individuals: the first at the young age (K1-K3) and the second in the spring of the second year of life (K0). In the first period of post-weaning growth (up to lens mass 2.25-2.50 mg or the age of 35-40 days) the rates varied among the seasonal cohorts (fig. 2). The rate for spring-born K1 was the highest (0.71 g per day), followed by K2 (0.40 g per day) and K3 (0.28 g per day).

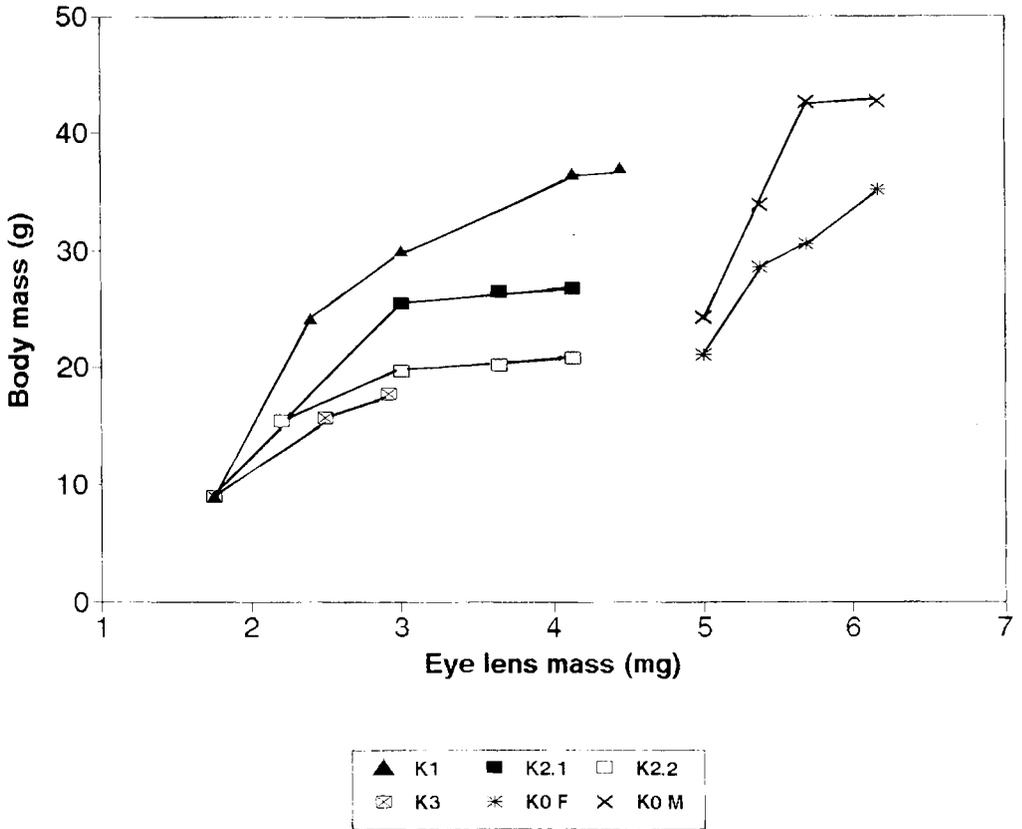


Fig. 2. Growth curves of the seasonal cohorts of the root vole. For overwintered individuals (K0): F. Females; M. Males.
 Curvas de crecimiento de las cohortes estacionales de topillo nórdico. Para los individuos (K0): F. Hembras; M. Machos.

After the initial phase of growth, K1 individuals continued to grow to the end of the breeding season, while they reproduced intensely at the same time. The majority died before September and only a few met the approaching winter as large individuals (38-40 g) in poor physical condition. None of them survived winter during the three years of the study (Gliwicz, unpubl.).

Among K2 individuals in July, matured voles were significantly heavier than the immature individuals (table 1). However, neither mature nor immature K2 voles

showed further growth for the rest of the breeding season (fig. 2). Their body masses at the end of the breeding season were about 26 and 21 g, respectively. Exactly the same pattern of growth inhibition was observed in marked individuals recaptured after July in live traps.

K3 young continued to grow, but since little time remained to the end of the season and their growth from the beginning was slow, they met winter at a significantly lower body weight than K2.2 individuals (17.3 and 20.9 g respectively) ($t = 5.45, df = 19, p < 0.001$).

Table 2. Comparison of growth and maturation of seasonal cohorts in four European vole species.

Comparación del crecimiento y maduración en cohortes estacionales de cuatro especies de topillos europeos.

	Species			
	<i>M. oeconomus</i> N. Poland this paper	<i>M. agrestis</i> S. Finland MYLLYMAKI (1977)	<i>M. arvalis</i> W. France MARTINET & SPITZ (1971)	<i>C. glareolus</i> Moravia, CR ZEJDA (1971)
No. of groups with different growth rates	3	3	3	3
Month of birth				
1st group	III-IV	V	III-V	III-V
2nd group	V-VI	VI	VI-VIII	VI-VIII
3rd group	VII-IX	VII-IX	VII-VIII	IX-XI
Inhibition of 2nd group				
growth	Yes	Yes	Yes	Yes
maturation	Yes	Yes	no data	Yes
Time	July	July	July	July

Interspecific comparison

In three other studies of European voles, in which the summer cohort was identified, a wide assortment of species and latitude was represented; that included *M. agrestis* in southern Finland (MYLLYMAKI, 1977), *M. arvalis* in western France (MARTINET & SPITZ, 1971) and *C. glareolus* in Moravia, Czech Republic (ZEJDA, 1971).

M. oeconomus from Northern Poland is now also added (table 2). The comparison of the results of these studies indicates common features of growth and maturation processes of voles of the summer cohort (K2). Growth is inhibited, and only some individuals mature in the first season. The first signs of inhibition were observed in July, regardless of geographical location of the studied population.

Discussion

The results of this study (i) confirm well known differences in growth and maturation rates between spring born and autumn born voles, and (ii) add some new aspects to the knowledge of growth and maturation of summer-born voles. In particular, two features of their development should be stressed:

- some summer born young stopped maturing as early as the beginning of July, and remained immature to the end of the breeding season; whereas others of exactly the same age (and living at the same time in the same habitat) reached puberty and reproduce.

- growth in voles (mature and immature) stopped at the beginning of July and low body weights were maintained (21-

26 g in comparison to 38-40 g of fully grown K1 voles) throughout the rest of the breeding season.

These patterns of development of summer born voles (i) support the hypothesis of adaptive switching from fast to slow development in later born voles (as opposed to the hypothesis of direct environmental limitation of their development), and (ii) are in disagreement with predictions of existing models of optimal energy allocation to growth and reproduction.

Support for the hypothesis of adaptive switching

Inhibition of development in K2 individuals in the study area occurred before the deterioration of environmental conditions. In July, the temperature and photoperiod were superior to those met early in the spring by fast-growing and reproducing K1 young. Although the food quality was not assessed, it could not be a limiting factor, because under the same food conditions individuals of other cohorts continued to grow (K1, K3) and reproduced (K0, K1). Finally, the inhibition of growth and maturation among summer born individuals was reported from various locations in Europe to occur exactly at the same time of year, despite the fact that these locations differed in light and temperature, as well as in an availability of fresh green food, due to the latitudinal differences.

Mid-summer inhibition of growth and maturation is an adaptive change in the strategy of young voles in response to some environmental cue acting as a «warning signal». Since the response occurred in all studied species and locations soon after the summer solstice, it is possible that the cue is the change (from lengthening to shortening) in the day-light period.

The following scenario of this event is suggested: those individuals which experience the summer solstice as subadults,

switch from maximizing their immediate (seasonal) reproductive output to maximizing their life-time reproductive success, which can only be achieved after successful winter survival. Since that time they become very sensitive to surrounding conditions, such as the availability of high quality food, a good site for nest location, mild neighbors. These individuals which can easily fulfill their needs, start to reproduce immediately at the level which does not increase the risk of winter mortality, but those that experience any shortage, postpone maturation.

This interpretation may explain the presence in the same area of mature and immature individuals of the same age (the results of this study). In cyclic populations, where the proportion of mature and immature young varies from year to year, the individuals most variable in this respect are summer-born subadults (eg. HANSSON, 1984; BERNSTEIN et al., 1989).

It is not clear, however, why all K2 individuals, and particularly those that postpone maturation, also stop growing.

Growth inhibition versus models of optimal energy allocation to growth and reproduction

According to the theory of optimal allocation of energy to growth and reproduction (STEARNS, 1976; KOZŁOWSKI & UCHMANSKI, 1987; KOZŁOWSKI, 1992) an individual which postpones maturity for the season should continue to allocate all energy to growth, in order to meet the next breeding season in large body size. In voles the large body size seems to increase reproductive success. Larger female voles produce larger litters and/or larger offspring (NADEAU, 1985), and larger males compete better for access to oestrus females (COCKBURN, 1988; GLIWICZ, 1991). The pattern of growth of K2 individuals does not therefore seem optimal, as they stop growing long before the end of summer, and then grow intensely and reproduce

at the same time in the following spring. This means that the lack of further growth in the first breeding season must have an adaptive value for voles which have no chance to reproduce at all, or produce only few young before winter. Large body size must significantly decrease their chances for surviving winter. This possibility has been theoretically discussed and indirectly demonstrated for several rodent species (IVERSON & TURNER, 1974; MERRITT & MERRITT, 1978; STENSETH, 1978; WEBSTER & BROOKS, 1981; HANSSON, 1992).

Thus, the body weight which is optimal for reproduction in voles is probably too high for successful wintering, which accounts for the inhibited growth of summer-born individuals. The models of optimal energy allocation to growth and reproduction in biannual organisms (developed for species other than rodents) assume that survivorship of individuals from one reproductive season to the next is independent of body size and only the size for reproduction is optimized (see KOZLOWSKI, 1992 for review). These models should be modified accordingly to account for 'unoptimal' life history of summer-born individuals.

Resumen

Crecimiento y maduración en cohortes estacionales del topillo nórdico

Las diferencias estacionales existentes en patrones de crecimiento y maduración de los topillos pueden ser el efecto directo de factores ambientales cambiantes o respuestas indirectas, seleccionadas por la evolución, a señales ambientales.

El fin de este trabajo es examinar el crecimiento y la maduración en cohortes estacionales de poblaciones salvajes de topillo nórdico, *Microtus oeconomus*, e investigar las causas de tales diferencias.

Se distinguieron tres cohortes de jóvenes del año (K1-K3) y una de individuos mayores de un año (K0). Los jóvenes na-

cidos en distintas estaciones diferían en la continuidad del crecimiento a lo largo de la estación reproductiva y en la maduración. Los primeros signos de inhibición estacional de crecimiento y maduración en topillos jóvenes nacidos en verano (K2) aparecieron justo antes de mediados de julio.

La inhibición se interpreta como una respuesta adaptativa que aumenta las posibilidades del individuo de sobrevivir al invierno. Se discuten la posible señal ambiental a la que responden y las probables ventajas de no crecer más. Los modelos existentes de redistribución de energía óptima para crecimiento y reproducción, que no encajan con pequeños roedores, no parecen pues ser adecuados.

Acknowledgements

The author wishes to thank A. Kowalczewski, the Head of the Field Station of the Warsaw University for the use of facilities. I thank T. Ozimek for phytosociological characteristics of the study area, and to J. Kozłowski and J. Nelson for critical reading of an earlier draft.

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