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ENERGY BALANCE AND FOOD REQUIREMENTS OF ADULT VIPERS *VIPERA BERUS* (L.)

ABSTRACT: In the diet of vipers rodents predominate. The bank vole *Clethrionomys glareolus* (Schreb.) is the most common prey animal. Also frogs are rather frequently consumed. The calculated consumption is 349.8 kcal per adult individual per year, or 25 rodents, 6 frogs and few animals from other systematic groups. As the density of vipers in the study area was one individual per hectar, the impact of this predator on rodent population seems to be insignificant.

1. INTRODUCTION

In herpetological literature there are many data on feeding and food composition of vipers (Brehm 1893, Vainio 1932, Psenner 1939, Rammner 1956, Frommhold 1964). These authors mainly set up the check-lists of prey species. An analysis of the contribution of different prey species to the total food of the viper can be found in the papers of Saint-Girons (1952), Pielowski (1962) and Prestt (1971). Food requirements of captive vipers was studied by Saint-Girons (1952). Data on the duration of feeding period for different age and sex classes in viper populations throughout the year have been reported by Prestt (1971). Metabolic rate was determined by Pomianowska (1972). Little information has been published, however, on bioenergetical indices for reptiles, and on the role of vipers in the biocenosis.

This paper presents the energy balance and food composition of the adult viper *Vipera berus* (L.). On the basis of these data, food requirement of the viper is calculated to determine the role of this predator in a natural biocenosis.

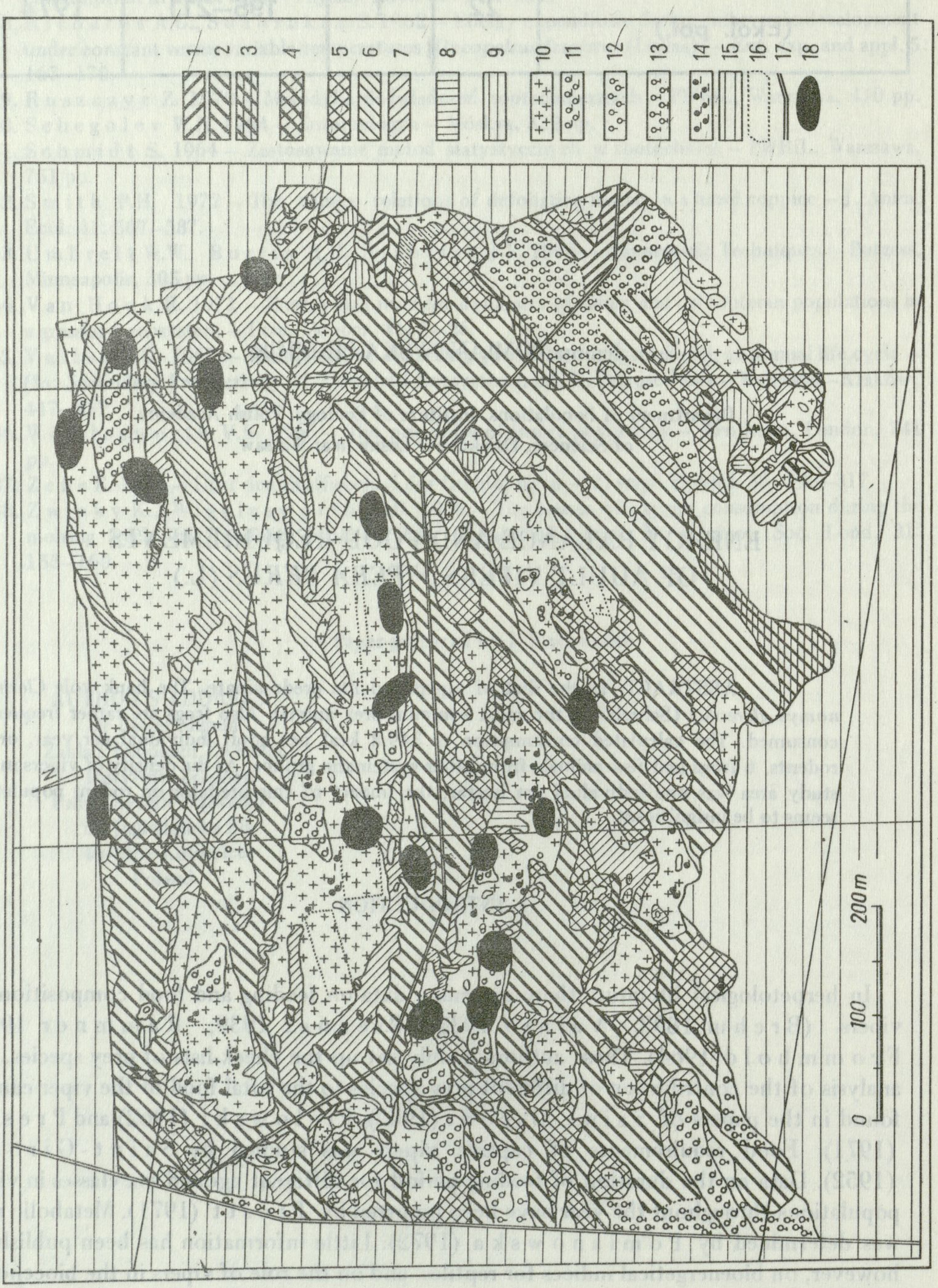
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Fig. 1. The map of the plant associations on the Strzeleckie Meadows (after T r a c z y k 1966) and the distribution of vipers

1 — *Glycerietum maximae*, 2 — *Caricetum elatae*, 3 — *Caricetum elatae* variant with *Phragmites communis*, 4 — *Caricetum elatae* variant with *Glyceria fluitans*, 5 — *Caricetum paradoxae*, 6 — *Caricetum gracilis*, 7 — *Carici-Agrostetum caninae*, 8 — *Carici-Agrostetum caninae* variant with *Calamagrostis neglecta*, 9 — *Carici-Agrostetum caninae* variant with *Calamagrostis canescens*, 10 — *Stellario-Deschampsietum*, 11 — wooded patches of *Stellario-Deschampsietum*, 12 — wooded patches of *Caricetum paradoxae*, 13 — wooded patches of *Caricetum elatae*, 14 — single trees, 15 — forest, 16 — cultivated plots, 17 — ditches, 18 — areas of viper occurrence

2. MATERIALS AND METHODS

The studies were carried out in three mid-forest meadows located in the Kampinos National Park, near Warsaw. These were Strzeleckie Meadows, Sierakowskie Meadows and Żabi Raj Meadows. They are covered with plant association of *Molinietalia*, *Magnocaricetalia* and *Caricetalia fuscae* orders, respectively. The surrounding forests consists of *Carici-elongatae-Alnetum*, *Vaccinio-myrtylli-Pinetum* and *Pino-Quercetum* associations (T r a c z y k 1966).

In the Strzeleckie Meadows (Fig. 1) the materials were collected in a plot of 10 x 400 m situated at the north-east edge of the meadow and forest, and in plots of a total area of 10.5 ha containing wooded patches scattered throughout the meadow. In the Sierakowskie Meadows vipers were collected from a plot of 10 x 1200 m, situated at the edge of the meadow and forest. In the Żabi Raj Meadows they were collected from a plot of 5 x 400 m. The size of the plots was assessed on the basis of the preliminary observations of viper occurrence.

The studies were conducted from the end of May to September, 1970, and from April to September, 1971. In the Strzeleckie Meadows observations were made once a week in April and May, and 2–3 times a week in other months. The vipers were regularly caught and removed from the plots to estimate their numbers. In the other areas capture was not so regular and was limited to the narrow belts where vipers mostly occured. They were collected to obtain supplementary materials used for dissection or keeping in captivity. Also some information was obtained on the duration of the activity period of vipers in the field. The number of vipers captured in successive months is presented in Table I.

Tab. I. The number of vipers caught in the Strzeleckie Meadows during 2 seasons

Month	Number of vipers	
	1970	1971
April	–	19
June	–	8
July	19	18
August	34	4
September	2	2
Total	55	51

The captured individuals were killed with chloroform, weighed to the nearest 1 gram, and then the content of their digestive tracts was examined to determine the species composition of food and the duration of feeding period over the year. Also the data on sex ratio, proportion of pregnant females, the number of eggs and the weight of embryos were obtained from these materials.

A part of the individuals caught in 1971 (12 females and 2 males) was kept in an enclosure of the size of 4.5 x 9.0 x 2.0 m, situated in a pine forest. The bottom and lower parts of the side walls were covered with concrete. The upper parts of the walls and the roof were made of a mesh screen to protect the vipers against possible predators.

Within the enclosure there was a concrete ditch filled with water. Sand and peat was spread on the bottom. In addition, there was a heap of litter there, clusters of grasses and sedges in water, bricks and stones. Since the enclosure was situated under the pine canopy and a major part of it was significantly shaded, an electric radiator, such as used in poultry farms, and an infra-red radiator of 300 W were installed.

To determine the duration of hibernation period, a ground was prepared where the vipers could hibernate. This was an excavation of a size of 1 x 1 m, 2 m deep, filled with peat, litter, snags of wood and dry branches. It was connected with the enclosure. From 9 individuals entering hibernation, 6 survived to spring.

The captive vipers readily preyed on supplied frogs, *Rana arvalis* Nil. and *Rana temporaria* L., and on laboratory mice, *Mus musculus* L., although they killed more individuals than consumed. All captive vipers were individually marked with white paint. After shedding the paint marks were replaced. 9 captive females gave birth to a total of 86 young. All captive vipers were weighed 7 times during the experiment (from June 22 to Semptember 14) and the increase in the body weight of adults was calculated.

A feeding experiment was made in captivity to find assimilation efficiency. Glass terraria supplied with water and placed within the enclosure were used in this experiment. A viper was starved in each of them for several days and then it was supplied with a living mouse *M. musculus* of known weight. Since that time feaces were collected once a day. Calorific values of all materials, i.e., adult vipers in spring and autumn, new-born vipers (in summer), young vipers after hibernation (in spring), sloughs and faeces, were measured with Berthelott calorimeter, KL-3 type.

3. ENERGY BALANCE

Energy balance was calculated for an individual of average weight for the studied population per year.

The duration of the hibernation period was determined from observations in the field and captivity. The first vipers were recorded on April 19, 1970, March 21, 1971, and April 1, 1972. So, it was accepted that the hibernation period generally extends to the end of March. The latest vipers were observed in the field on September 15, 1970 and October 13, 1971; it was assumed that they generally start to hibernate in October. In captivity some vipers entered hibernation at the end of September and others only in late October. They emerged during April 5–20 in spring.

Both post-mortem examinations, from which the number of vipers with empty and full stomach in successive months (Tab. II) was obtained, and average temperatures of the day and night indicate that feeding generally occurs during four months of the year (from May to August).

Tab. II. The number of individuals with empty and filled guts during the seasons of 1970 and 1971

		Month						
		April	May	June	July	Aug.	Sept.	Total
Guts	empty	22	4	1	22	18	3	70
	full	1	6	6	26	23	1	63

S k o c z y l a s (1970), who was dealing with the effects of temperature on food digestion in the grass snake *Natrix natrix* (L.), suggests that a temperature of 15°C is too low to the normal digestion because enzyme action is inhibited. Also the amount of digestive juices secreted at 15°C is low. Average daily temperatures in April and September were below 15°C (unpublished data of the Institute of Ecology, PAS). Assuming that the effect of temperature on the digestion rate for the viper and the grass snake is similar, it can be expected that vipers feed from May to August, although it may happen that under favourable thermal consitions they take food in April or September. But the observations in captivity indicate that the food is regurgitated when the temperature drops, sometimes several days later, without any signs of being digested or only slightly digested. To calculate the productivity of vipers, the following parameters were considered: an average gain in individual body weight, epidermis production, the body weight of young born in captivity, and calorific value of the body and sloughs (Tab. III). It was assumed that the body weight increased uniformly over the feeding period. Data on the duration of the captivity period and on the gain in the body weight during that time were used to

Tab. III. Calorific value of the body of adult vipers at the beginning and at the end of the season (April-September) and calorific value of young and sloughs

	Beginning of the season		End of the season		Young		Sloughs
	♀♀	♂♂	♀♀	♂♂	new born in summer	after hibernation in spring	
Weight (g)	80.6	47.4	92.7	58.0	5.0	5.0	0.8845
cal/g f.wt	1190.4		1746.3		1106.2	2033.4	5748.6

calculate the average increase in the body weight per day. Assuming that the feeding period lasts 123 days a year, the average increase in the body weight was calculated for that period (Tab. IV).

Basing on the data on fat reserve in pregnant females (P r e s t t 1971) it was accepted that there is no increase in their body weight if the increase due to egg production is not taken into account. For that reason the annual increase in the body weight for females giving birth during the season was estimated as a difference between the latest measurement before hibernation and the first measurement after giving birth.

The average increase in the body weight of captive individuals throughout the season was 12.1 g for females and 10.6 g for males. Comparing the average weights and calorific values of vipers (in cal/g of fresh weight) it was possible to calculate the tissue production in energy units throughout the season. It is 65.93 kcal per female and 44.86 kcal per male.

The weight of new-born individuals was calculated as a difference between the last weight of the female before giving birth and the first weight after. The weight of a female after giving birth decreased by 61 g on the average. This is an average value for 9 females (Tab. IV). The average weight of a new-born viper is 5 g, so one female gives birth to 12 individuals, on the average. This is the equivalent to 122 kcal produced by a female. The weight of fetal membranes was not considered here. Data obtained from post-mortem

Tab. IV. Increase in the body weight of captive vipers

No.	Body weihgt							Difference between final and original weight*	Difference in weight before and after giving birth
	June 22	July 13	July 23	Aug. 3	Sept. 13	Aug. 25	Sept. 14		
♀♀									
1	225	241	243	139**	150	142	152	13	104
2	143	139	151	119**	93	90	80	–39	32
3	58	125	123	133	68**	88	105	37	55
4	104	111	121	81**	69	63	93	12	40
5	124	146	143	77**	82	99	86	9	66
6	133	156	147	110**	115	104	112	2	37
7	141	139	141	61**	95	110	113	52	80
8		74	67	71	–	69	79	5	–
9		140*	141	142	70**	106	93	23	72
10		59	55	42	48	55	52	–5	–
11			153	145	85**	97	83	–2	60
12			51	56	–	63	65	14	
$\bar{x}$ for the total feeding period (123 days)								12.1	61
♂♂									
13		34	32	40	42	37	39	5	
14				72	84	79	77	5	
$\bar{x}$ for the total feeding period (123 days)								10.6	

*For pregnant females this is the difference between the last weight before and the first weight after giving birth.

**Giving birth.

examination of 34 pregnant females indicate that one female gives birth to 10 newborn on the average (Tab. V). In captivity 9 females gave birth to 86 newborn, i.e., to two newborn less than it could be expected from the measurements of the female body weight. This defference probably results from neglecting the weight of fetal membranes, fetal juices and the remains of yolk.

Tab. V. The number of foetus found in dissected females

The number of foetus per female	The number of females
5	2
6	3
7	5
8	3
9	3
10	2
11	7
12	2
13	2
14	3
15	1
17	1
$\bar{x}$ 10	Total 34

As it has already been mentioned, the activity period in vipers averages 6 months depending on the thermal conditions during the season. In captivity 50% of all individuals sloughed their skin within a fortnight, so it can be said that vipers generally slough once a month and they can slough 6 times during 6 months. Vipers were kept since June but it is quite sure that the first shedding occurs in April because fresh sloughs were found in the field at that period during two seasons.

The energy content of 6 sloughs averaged 30.5 kcal/individual per year.

On the basis of all data obtained, the value of production in energy units was calculated. It amounts to 146.9 kcal/individual per year.

The daily metabolic rate of the vipers was calculated from the previously published data (Pomianowska 1972). The amount of oxygen consumed by a viper per year was calculated taking into consideration the differences in mean monthly air temperatures in the Kampinos Forest region for the period of viper activity, and the differences in the ground temperatures to the depth of 50 cm (Annals of the ground temperatures — Institute of Meteorology and Water Economy) for hibernation period. In this way a mean annual resting metabolic rate was found. The metabolic rate of active animals is correspondingly higher. In the available literature there is no information on the differences between the resting and active metabolic rates for vipers. Benedict (1932 cited by Templeton 1970) found that the metabolic rate of the active tortoise *Testudo* *denticulata* increased 3.5 times as compared with its resting metabolism. Basing on the observations it was assumed that vipers are active only 3 hours a day. Including all these corrections it was calculated that under the conditions prevailing in the Kampinos Forest, metabolism of the viper averages 155 kcal per year (Tab. VI). Adding the calculated annual values of production to respiration, energy assimilated during the year was calculated for an average individual. It is 301.9 kcal. Assimilation efficiency, A/C, found in the feeding experiment averages 86.3% (Tab. VII). Using this value, food consumption was calculated and the amount of faeces dropped by an individual of average weight in the viper population per year (Tab. VIII).

Tab. VI. Respiratory rate of an adult individual during the year

Month	Mean ambient temperature (^{o}C)	Respiration (ml O_2/g per 24h)	Mean body weight (g)	Respiration* (kcal/individual)
X–III	5	0.70	79	48.2
IV	8	0.84	54	8.2
V	13	1.10	79	16.9
VI	18	1.40	79	20.8
VII	19	1.46	79	22.3
VIII	18	1.40	79	21.5
IX	14	1.16	79	17.1
			Total	155.0

*Including energy losses for locomotor activity.

Tab. VII. Assimilation of food by vipers fed on *Mus musculus* of a calorific value 2.25 kcal/g fresh weight

No.	Consumption		Faeces			Assimilation	
	g	kcal	g	kcal/g	kcal	kcal	$\frac{A}{C} \cdot 100\%$
1	20	45.00	3.04	1.90	5.78	39.22	87.1
2	22	49.50	3.20	2.05	6.57	42.93	86.7
3	25	56.25	3.46	2.00	6.93	49.32	87.7
4	28	63.00	4.01	2.11	8.46	54.54	86.6
5	31	69.75	5.10	2.12	10.81	58.94	84.5
6	32	72.00	5.08	2.12	10.77	61.23	85.0

Consumption calculated for an individual of the average weight in the population is 349.8 kcal, and assimilation is 301.9 kcal. Assimilation efficiency is slightly lower than for small predators. K o z l o v s k y (1968) found that assimilation efficiency for the

Tab. VIII. Energy balance of an individual during the year

Production (kcal)	Respiration (kcal)	Assimilation (kcal)	Faeces + urine (kcal)	Consumption (kcal)
146.9	155.0	301.9	47.9	349.8

trophic level of invertebrate predators exceeded 90%. A similar value, which amounts to 90%, has been reported by M o u l d e r et al. (1970) for spiders.

Cumulative coefficients of production efficiency, P/C and P/A, calculated for an adult viper per year amount to 41.9% and 48.6%, respectively. K o z l o v s k y (1968) found that for invertebrate predators P/C is 32–38% and P/A is 31–37%, so they were slightly lower than those found for the viper.

4. FOOD REQUIREMENTS

During two seasons 127 killed vipers were examined, 56 of which had food in the guts and 71 did not (Tab. II). In addition, 7 samples were taken from living individuals which were forced to regurgitate their food.

Because the obtained prey animals were often digested to a high degree, not all species could have been indentified and sometimes it was only possible to determine their class (birds, insects etc.). Nor it was possible to identify the species of young rodents (taken from their burrows). In 63 samples there were at least 11 species of animals from various systematic groups (Tab. IX). 44 individuals per 63 contained one prey animal in the guts. It was also observed in captivity that the viper having taken a frog or a mouse usually did not take any food for several following days.

9 vipers took 2 or more prey of the same species. In 3 cases more than two prey animals were taken, namely, in two cases 4 and in one case 3 suckling mammals were taken from the burrow. In one case two nestlings were taken. In five cases two adult individuals were taken at short intervals; these were frogs, lizards and voles. The observations of captive vipers also indicate that they occasionally take up to 7 new-born mammals or two adult mice.

10 vipers took 2 prey animals each belonging to a different species in the following combinations: a vole and a frog (6 times), a vole and a lizard (once), a lizard and a frog (once), a vole and the yellow-necked field mouse (once), a frog and a beetle (once).

To determine the real contribution of different prey species to the viper food, which can not be found if only the number of eaten prey animals is available (G o s z c z y ń s k i 1972), the results have been presented in weight percentages (Tab. IX).

The weight of food in grams was calculated by multiplying the number of prey animals found in viper guts by the average weight of each species. It was the average weight of living animals (B a b i ń s k a 1972, Pomianowska-Pilipiuk – unpublished data).

Rodents predominate in the diet of vipers (Fig. 2). They contribute to almost 74% of the total food. Also frogs are important prey animals. Among rodents the bank vole *Clethrionomys glareolus* (Schreb.) is the most common prey.

Tab. IX. Species composition of the food of vipers

Species		Number of samples*	Number of individuals	Mean body weight (g)	Food biomass (g)	Per cent of weight	Index of frequency (%)
Rana sp.		20	22	7.0	154.0	15.86	25.9
Clethrionomys glareolus		17	21	21.7	455.7	46.94	24.7
non-specified rodents	ad.	4	4	22.0	88.0	9.06	4.7
	juv.	7	14	3.0	42.0	4.33	16.5
Lacerta sp.		8	10	3.0	30.0	3.09	11.8
Microtus sp.		3	3	24.5	73.5	7.57	3.5
Sorex sp.		3	3	7.8	23.4	2.41	3.5
Aves		2	3	15.0	45.0	4.63	3.5
Apodemus flavicollis		2	2	24.4	48.8	5.03	2.3
Micromys minutus		1	1	8.2	8.2	0.84	1.2
Anguis fragilis		1	1	2.0	2.0	0.21	1.2
Coleoptera		1	1	0.2	0.2	0.02	1.2
Total		69	85		970.8	100.00	100.0

*The number of vipers in which the particular prey species were found.

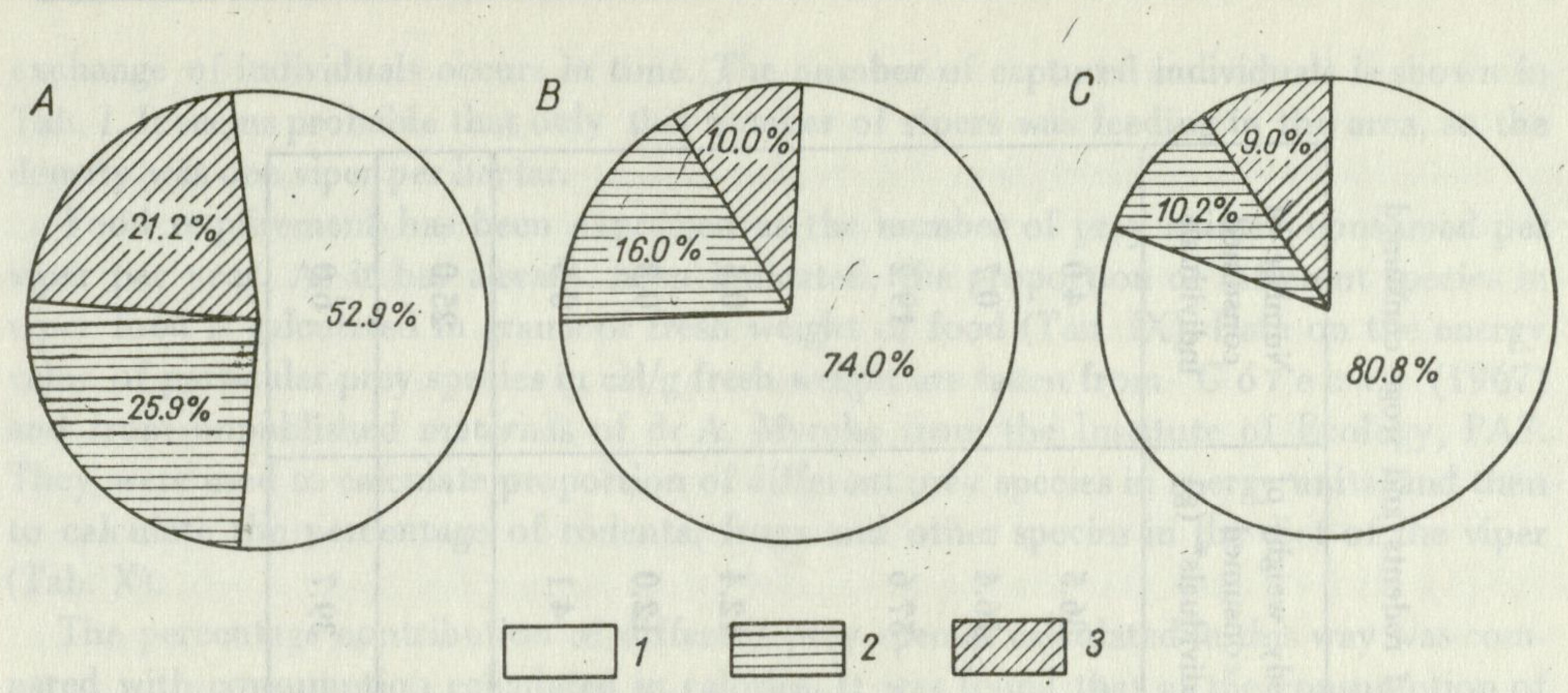

Fig. 2. Contribution of different groups of animals to the food of the viper calculated as: *A* – per cent of the total number of prey animals, *B* – per cent of weight, *C* – per cent of energy value

1 – rodents, *2* – frogs, *3* – other animals

As it has already been mentioned, the number of vipers was also determined in the Strzeleckie Meadows. The observations of each individuals were mapped. It can be seen that vipers have clumped distribution throughout the meadow (Fig. 1). The Strzeleckie Meadows cover 66 ha but all individuals were observed on the area of about 12 ha. It is possible, however, that the vipers penetrate the whole meadow and only stay at particular sites gathered together as they are not territorial animals (Vainio 1932, Pielowski 1962, Prestt 1971). Pielowski (1962), Parent (1968) and Prestt (1971) found that vipers have definite territories and they rarely migrate during the summer period. Only in spring and autumn, when they move to hibernation sites or come back to the summer sites, they may cover a distance of 800–1500 m. During the summer period they can always be found in the same places. So, it was assumed that despite removing there was neither immigration of new individuals to the area nor emigration, although occasionally both the phenomena could take place. The fact that not all individuals were caught within a short time period need not indicate that new individuals were still coming to the area. As Pielowski (1962) has found, only a part of the population stays on the ground surface and the

Tab. X. Percentage contribution of different groups of animals to the food of a viper of average size; it is calculated from the calorific value of their biomass (data from the analysis of gut content during two seasons)

Food	Total weight of food (g)	Energy content of the body (cal/g)	Energy content of the food biomass	
			kcal	%
Rodents	716.2	1526	1092.9	80.8
Frogs	154.0	898	138.3	10.2
Others	100.6	1200	120.7	9.0
Total	970.8		1351.9	100.0

Tab. XI. Food requirements of the viper throughout the year calculated as the number of rodents and frogs consumed

Rodents		Per cent of individuals	Food biomass (kcal)	Calorific value (cal/g f. wt)	Body weight of consumed individuals* (g)	Number of consumed individuals
Clethrionomys glareolus		46.7	132.0	1526	86.5	4.0
Non-specified rodents	ad.	8.9	25.1		16.4	0.7
	juv.	31.1	87.9		57.6	19.2
Microtus sp.		6.7	18.9		12.4	0.5
Apodemus flavicollis		4.4	18.4		12.0	0.3
Micromys minutus		2.2	6.2		4.1	0.5
Total		100	282.6			25.0
Frogs		100	35.7	898	39.7	6.0

*The average body weight, see Table I.

exchange of individuals occurs in time. The number of captured individuals is shown in Tab. I. It seems probable that only this number of vipers was feeding in the area, so the density was one viper per hectar.

Food requirement has been expressed as the number of prey animals consumed per viper per year. As it has already been indicated, the proportion of different species in viper food is calculated in grams of fresh weight of food (Tab. IX). Data on the energy value of particular prey species in cal/g fresh weight are taken from G ó r e c k i (1967) and from unpublished materials of dr A. Myrcha from the Institute of Ecology, PAS. They were used to calculate proportion of different prey species in energy units, and then to calculate the percentage of rodents, frogs and other species in the diet of the viper (Tab. X).

The percentage contribution of different prey species calculated in this way was compared with consumption calculated in calories. It was found that at the consumption of 349.8 kcal per individual per year, 80.8% of energy of 282.6 kcal is due to rodents, 10.2% or 35.7 kcal to frogs and 9% or 31.5 kcal to other species taken as food (Fig. 2).

Data on rodents and frogs are discussed in details. The prey species from other systematic groups are neglected because they are highly diversified and low in numbers.

Knowing the amount of energy taken in the form of frogs and the calorific value of a frog, it has been calculated how many grams of frogs are consumed by a viper. From the weight of frogs found in the guts, the number of individuals taken by vipers was calculated (Tab. XI).

The data on prey rodents were treated in the same way, the only difference being that the calculations were made for each species separately. Thus, having the total number of rodents found in the guts, the percentage contribution of particular species was calculated. Then, basing on the previous calculations, it was assumed that 282.6 kcal equals 100%, and the percentage contribution of each rodent species was calculated in calories. The obtained results (Tab. XI) indicate that an adult viper can consume, during 123 days from May to August, 6 adult rodents, 19 suckling rodents and 6 frogs on the average, not including additional food. Since it has been found that there is one viper feeding per hectar of the meadow, then the consumption calculated per hectar is exactly the same.

5. DISCUSSION

There are some sources of errors in the calculation of energy balance. First of all, the captive females were more numerous than the captive males. Only two males were used to calculate the average value of production because others were kept too short. In addition, the vipers were not starved before being weighed, which might affect their real weight. Only the latest measurements were taken for starved individuals.

Metabolic rate was measured in summer, and the results were calculated for a year, which also accounts for an error. It is known that there are differences in the metabolic rate of poikilothermic vertebrates between the summer and winter periods at the same ambient temperature of 5°C. In addition, the vipers were adapted to the ambient temperature only for 2 hours. As S k o c z y l a s (1969) pointed out when dealing with the temperature of the grass snake stomach, this is a sufficient period of adaptation at the ambient temperature of 25 and 15°C but unsufficient period to lower the temperature of the animal to an ambint temperature of 5°C. Besides, seasonal variability, which is certainly significant is not taken into account.

Faeces were not collected immediately after being voided, so they were dried a little. The vipers kept in terraria were supplied with one mouse only, which could affect the rate of food movement, and hence the rate of defecation. Perhaps stress resulting from keeping the animals in small terraria had also some effects.

The estimate of energy lost due to the activity of vipers can also account for an error because the increase in metabolic rate in an active tortoise is likely to be different from that in an active viper.

The timing and duration of hibernation is comparable with the results of Prestt (1971). He has found that the beginning of the active period falls into the end of February and it is finished in early November. So, the differences between Great Britain and Poland are not large and they probably result from the differences in climatic conditions.

There are significant differences in food composition between the present results and those reported by Saint-Girons (1952). In viper food in France there is no species predominating here, i.e., *Rana* sp. and *C. glareolus.* There are other species instead, such as *Crocidura* sp. (Wagler), *Apodemus silvaticus* (L.), *Arvicola terrestris* L. and several species of birds.

These results are in accordance with those obtained by Pielowski (1962) from materials also collected in the Kampinos Forest. Some differences in the food quantity and composition are due to several reasons. Firstly Pielowski (1962) examined food obtained exclusively from living individuals, so smaller prey animals could not be detected; the shape of the viper did not indicate that it contained food. For that reason the number of prey species found by Pielowski (1962) was 6, while 11 were recorded here. Besides, Pielowski (1962) collected materials in the forest, while the majority of samples (50) analysed here was collected in meadows.

On the meadows under study *Apodemus agrarius* (Pall.) is a predominant and characteristic species, while in the forest *C. glareolus. Apodemus flavicollis* is a rodent overlapping from the forest into the meadows, while *Microtus arvalis* overlaps from the meadows into the forest. Since voles, which predominate in the viper diet, are very sparce in the meadows (Babińska 1972) and abundant in the forest (Andrzejewski 1963), it could be supposed that vipers prey upon in the forest or at the edge of the meadow and forest, taking mainly individuals migrating onto the meadow.

Also according to Pielowski (1962), the majority of vipers feeds on voles. This author has also found *A. agrarius* in the diet of vipers. This species has not been found in the examined samples, although it is numerous in the study meadows (Babińska 1972). The fact that the vipers inhabiting both the meadows and the forest feed mainly on voles may indicate that there is some food preference in vipers. Perhaps it is also related to behaviour of this prey species and its response to the presence of predators, which may be different than in other rodents.

Pielowski (1962) suggested that mainly migrating animals were taken by vipers. Basing on this suggestion, it can be stated that high proportion of voles in viper diet results from the fact that this is a migratory species in the meadows.

Preying on several individuals of different species at short intervals is reported by Prestt (1971). He found even 3 adult prey animals of different species in one viper stomach. In seems to indicate that in the field vipers still continue to prey upon if only there is an opportunity, although they have their stomach full. It was observed in captivity that the mouse beaten by a viper can run away to such a distance that the viper can not find it despite the efforts. This is possible because generally the viper awaits motionless for a while and then approaches the prey. It rarely happens that the viper approaches the prey immediately after having beaten it, even if the latter makes efforts to escape. It is not known to what extent the behaviour of captive vipers is modified as compared with free-living vipers but also in the field they are likely to kill more prey than to consume because they are not able to find all killed animals. However, when they manage to find them, they take several prey at short intervals.

To find the food requirements of the viper, the average fresh weights of prey species were used. This was, for instance, an average weight of individuals in the rodent population inhabiting the Strzeleckie Meadows (not including individuals not leaving their burrows). The prey animals found in the guts were generally considerably digested and their weight could not be compared with the weight of living individuals. In this respect the average weight of individuals in the population was used, which must have accounted for some errors because the impact of a predator on particular components of prey population is not generally uniform. It is possible that mainly young individuals, which are not so heavy as adults are preyed upon, or pregnant females, which can not escape so easily are taken, or migrants (P i e l o w s k i 1962). Also the estimate of the number of vipers is not precise. Not absolutely all individuals could be caught because some of them were hidden and some could immigrate into the plot.

The flow of rodents through the meadows is considerable. In 1970 B a b i ń s k a (1972) marked 327 individuals of six species on a hectar plot (186 *A. agrarius*, 2 *C. glareolus*, 6 *A. flavicollis*, 81 *Microtus* sp., 16 *A. terrestris*, 36 *Micromys minutus* (Pall.)). Thus, this is approximately the size of rodent population subjected to exploitation by vipers. If the impact of the viper population (which takes 30 individuals from 327 present) would be the same for all the species, it could be estimated as being low even if the values obtained in this paper differed severalfold from real ones. Since the contribution of voles to the viper diet is the highest and, according to the calculated food requirement, a viper takes 5 voles per ha per year, it can be suggested that the effect of vipers on this species is significant in the study area.

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6. SUMMARY

Assimilation efficiency in vipers was found from feeding experiments. (Tab. VII). Production was determined by measurements of the body weight and its calorific value throughout the year. The energy value of sloughs and energy requirement for reproduction were also included. Respiration values were taken after Pomianowska (1972). Those data were recalculated taking into account the actual temperature conditions and activity of vipers throughout the year (Tab. VI). Basing on the production, respiration and assimilation, the consumption of an adult individual per year was calculated (Tab. VIII).

The species composition of prey animals was found by examining the stomach content. Rodents predominate in the diet of the viper, C. glareolus being the most abundant prey species (Tab. IX). Basing on the calorific values of both consumption by vipers and prey animals of particular species, and also taking into account the frequency of the occurrence of particular prey species in the food, their number consumed throughout the year was calculated (Tab. XI).

Knowing the number of vipers in the area under study (Tab. I) it was possible to determine their impact on the rodent population per hectar.

7. POLISH SUMMARY (STRESZCZENIE)

Na podstawie pokarmowych eksperymentów hodowlanych określono współczynnik asymilacji pokarmu przez żmije *Vipera berus* (L.) (tab. VII). Produkcję oceniono badając przyrost ciężaru ciała i jego wartość kaloryczną w ciągu sezonu, wartość energetyczną zrzucanego naskórka, a także uwzględniono wydatki energetyczne związane z urodzeniem młodych. Respirację przyjęto za pracą Pomianowskiej (1972). Dane te przeliczono, uwzględniając warunki termiczne i aktywność zwierząt, na wielkość respiracji dorosłego osobnika w ciągu roku (tab. VI). Znając tak wyrażoną wielkość produkcji i respiracji oraz współczynnik asymilacji pokarmu określono konsumpcję jednego dorosłego osobnika w ciągu roku (tab. VIII).

Badając zawartość żołądków dorosłych osobników ustalono listę gatunków wchodzących w skład pokarmu żmij. Dominującą rolę w pokarmie żmij odgrywają gryzonie, szczególnie *Clethrionomys glareolus* Schreb. (tab. IX). Z wyliczonej na podstawie bilansu energetycznego konsumpcji oraz z wartości energetycznej zjadanego pokarmu, przy uwzględnieniu częstotliwości występowania poszczególnych gatunków w pożywieniu, określono liczbę zjadanych przez żmije zwierząt poszczególnych gatunków w ciągu roku (tab. XI).

Znając liczebność żmij na określonym terenie (tab. I) można było ocenić ich wpływ na populację gryzoni na hektar.

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