Energy Flow through the Common Hamster Population

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A study of the energy flow through a population of the common
hamster *Cricetus cricetus* (L i n n a e u s, 1758) and its impact on
crops was carried out in cultivated fields, 128 ha in area, in the Vistula
valley, about 80 km east of Cracow. The population dynamics of these
rodents, their activity rhythm, and the climatic parameters were
determined in a field study. The average daily metabolic rate (*ADMR*)
and chemical thermoregulation (*RMR*) were measured in the laboratory,
where the composition of their natural diet and the consumption and
utilization of foods were also estimated. The number of adult hamsters
was determined by counting active burrows in the spring and autumn
of each year. The mean annual density of adult hamsters was 8.5/ha.
After the inclusion of young animals, the number of which was
estimated from the number of embryos, the total annual density is on
the average 12.4 hamsters/ha. The daily energy budget (*DEB*) of an
average hamster in each month of the year was calculated from the
measurements of the dependence of *ADMR* upon body weight, *RMR*,
and the data on metabolism during hibernation obtained from literature.
DEB reaches the highest level in the months of activity (on the average
about 40 kcal/animal day). *DEB* fluctuates between 11 and 30 kcal/ani-
mal day during hibernation. The whole population dissipates a total of
1.44×10^5 kcal/ha year for the cost of maintenance (respiration), 83%
of which in the period of active life. The production of the population
is 1.12×10^4 kcal/ha year and its efficiency in relation to assimilation
is 7.2%. The impact exerted on crops by the summer consumption of
hamsters is small and constitutes less than 1%. On the other hand, the
losses caused in crops by their consumption in the autumn and chiefly
by the gathering of food supplies (about 15 kg/animal), reach 6%
and are the more important, because they mainly affect the final crop,
i.e. grain.

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I. INTRODUCTION

Recent observations have provided a large number of data necessary to
estimate the energy flow through animal populations. As regards mam-
mals, particularly much information in this respect has been gathered
about many rodent (G r o d z i ń s k i, K l e k o w s k i & D u n c a n, 1975;
G o l l e y, P e t r u s e w i c z & R y s z k o w s k i, 1975) and ungulate

(G r o d z i ń s k i & P u c e k, 1975) species. It should however be empha-
sized that all these papers are, as a rule, concerned with species that
are active continuously all through their lives.

However, there are a great many periodically active mammals. Their
significance is indicated by the fact that, out of the about 100 species
living in Poland (K o w a l s k i, 1964), more than 40 species »withdraw«
from active life for a variously long time either in the daily or in the
annual cycle. In addition to hibernators, this group includes estivating
species and such as can change their metabolism very considerably
during the 24-hour period, *e.g.* bats, which occur in large numbers in the
Polish fauna, or some small rodents. The flow of energy through the
animals included in this group is incomparably worse known and even
then in hardly a few species (K a y s e r, 1939, 1961; G ę b c z y ń s k i,
G ó r e c k i & D r o ż d ż, 1972).

The periodically active animals, notably the hibernating species, differ
completely from the continuously active animals in their influence upon
the ecosystem, because the hibernators survive the whole year at the cost
of energy stored in the form of their own tissue or food supplies. This
storage of energy must be completed in the relatively short period of
their active life. The deposition of tissues is rather an energetic process
(B l a x t e r, 1966; K i n g & F a r n e r, 1961) and it raises the energetic
expenses of animals. In the same period of active life the animals must,
in addition, bear the very high cost of reproduction (K a c z m a r s k i,
1966; T r o j a n & W o j c i e c h o w s k a, 1967; M i g u l a, 1969).

The common hamster *Cricetus cricetus* (L i n n a e u s, 1758) is a rodent species,
which is active for only a part of the year and its body weight often exceeds
800 g. The range of this animal covers the whole steppe region of Eastern Europe
and in Asia it extends as far as the Yenisey. In Europe the range of the common
hamster is discontinuous, in the west and south it reaches Belgium, France,
Switzerland, Yugoslavia and Rumania (K o w a l s k i, 1964) and the northern border-
line of its distribution runs across FRG, GDR, and Poland. In Poland common
hamsters inhabit the southern and central parts of the country except the Carpa-
thians (S u r d a c k i, 1963, 1971, 1973). They live nearly exclusively in meadows and
cultivated fields. Being for the most part plant-eaters (S u r d a c k i, 1964; G ó r e c-
k i & G r y g i e l s k a, 1975), which gather proverbial winter food supplies (F e-
r i a n c o v a - M a s a r o v a & H a n a k, 1965; W a l k e r, 1964), the hamsters may
cause damage to crops, the more so, because building their extensive burrows,
they impede the mechanical cultivation of the soil. An additional feature is the
fact that, although hamsters are not marked by typical mass outbreaks, they
maintain the mean size of population at a relatively high level.

The ecology and biology of this species is known only fragmentarily (P e t z s c h,
1952; W a l k e r, 1964; K a r a s e v a & S h i l a y e v a, 1965; S a m o š, 1975; V o h r a-
l i k, 1974, 1975). Owing to their wide range, hamsters were used as models of hiber-
nating mammals. In this context the physiological data concerning these animals
are for the most part limited to the period of hibernation (K a y s e r, 1939, 1959,
1971; L y m a n & D a w e, 1960), whereas only little is known about their physiolo-

gical features during the period of active life, this being chiefly information on the consumption (S u r d a c k i, 1964) and utilization food by hamsters (E r d a k o v, 1972; G ó r e c k i & G r y g i e l s k a, 1975). Similarly, little information is available on the metabolism and thermoregulation of hamsters (K a y s e r, 1959, 1961; V i s i - n e s c u, 1968; M a l a n & H i l d w e i n, 1969; G ó r e c k i & W o ł e k, 1975) or their activity (C a n g u i l l e m, S c h i e b e r & K o c h, 1973; W e i n e r & G ó r e c k i, 1974).

In order to evaluate the flow of energy through the population of these animals and to estimate their role in the ecosystems of cultivated fields quantitatively, it was indispensable to get to know the missing links in their physiological, bioenergetic and population parameters. The purpose of the present work was to collect data concerning (a) the size and demographic parameters of a hamster population and (b) the growth rate and body weight of these animals. The 24-hour activity rhythm and the length of stay of hamsters out of their burrows were determined under field conditions. The daily metabolism and chemical thermoregulation were measured in the laboratory. The composition of food consumed and its utilization were also determined and the data on thermal conditions under which the study population lived were noted.

All the information obtained in this way made it possible not only to estimate the dynamics of the population size and some physiological indices of this rodent, but also to calculate the flow of energy through the whole population. Apart from this it became possible to determine, in part, the economic significance of the common hamster and the damage caused by it. This study, as a whole, enabled us also to grasp the differences between the rodents which are periodically and those permanently active.

II. MATERIAL AND METHODS

The present study of the energy flow through a hamster population was carried out during four successive years (1971—1974), applying both field and laboratory methods. All the field investigations were conducted in the fields of the Experimental Station, Institute of Tillage, Fertilization and Pedology, at Borusowa, about 80 km east of Cracow. At first the study covered an area of 200 ha and from the end of 1971 six complexes of fields of a total area of 128 ha. They were isolated from other fields by the embankment of the Vistula on one side and nearly completely by the buildings of the villages Borusowa and Karsy on the remaining three sides (Fig. 1).

The soils of these fields are silts on the substratum of loose sands and those with underlying clay. Despite the vicinity of the Vistula the water table is rather low; there was no water at the depth reached by the deepest burrows of hamsters more than 2 m. The main crops were wheat, maize, lucerne, rape, potatoes and sugar-beets; the singular fields did not, as a rule, exceed 20—25 ha in area. There were only very few trees amidst the fields. Dogs and a very small number of foxes were natural predators of hamsters in the study area.

The study was carried out in three complexes of fields each area comprising 50—70 ha the number of animals being estimated and observations made in two

of them (Fig. 1, fields Nos. 1 and 2). All captures were made in the control field
(No. 3).

The number of hamsters was estimated twice each year: in spring, immediately
after the hamsters had left their burrows, and in autumn, just before the hi-
bernation season. The number was determined by counting the burrows in several
to more than ten transects, 5 by 150 m each. The whole area in which the burrows
were counted was generally 2—7% (averaging 3.5%) of the area under a given
crop (Table 1). All the estimations were made simultaneously in two or three con-
secutive days over the whole area of 128 ha so as to eliminate the influence of
migrations of hamsters from one field to another at the time of counting.

Common hamsters generally live singly throughout the year with the one ex-
ception being that of nursing females (S a m o š, 1975; P e t z s c h, 1952). In addition
to its main burrow, usually with several entrances, each hamster has a few other
burrows used as hiding-places in a case of danger. They are scattered all over its
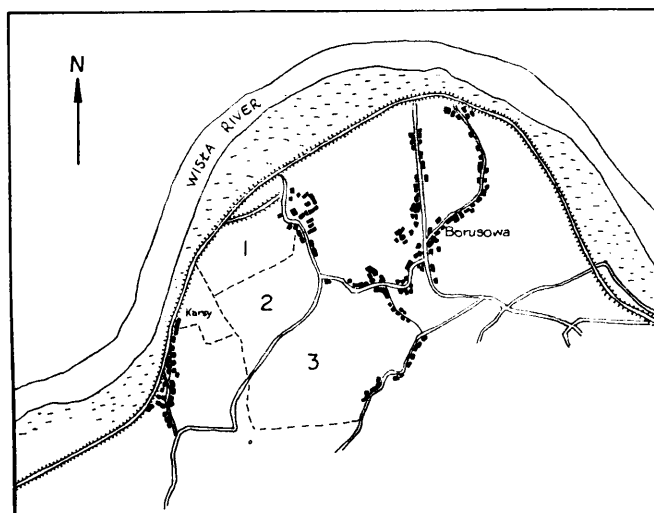

Fig. 1. Situation of the study area.
1, 2 — fields in which dynamics of the number of hamsters was studied, 3 — control
field, in which captures were made.

individual territory (K a r a s e v a & S h i l a y e v a, 1965). For this very reason, the
number of burrows (burrow entrances) falling to one animal was determined both in
the spring and in the autumn. The method used was that described by S u r d a c k i
(1968). At about 5 a.m. the entrances of 50—70 burrows were stopped with straw.
The size of the plots investigated in this way naturally depended on the number
of burrows and usually approximated 50×50 m. After 12 hours, and then in the
evening of the same day, and after 24 hours (in connection with the 24-hour
activity rhythm of hamsters) opened burrows were counted. The mean from the
two counts of opened burrows was used to calculate the ratio of the number of
opened burrows to that of closed ones. The index thus calculated was later used
to compute the number of hamsters and the number of active burrows in the
study area in the given season.

In order to find the age and sex structures of the population and to perform all

the laboratory determinations and measurements, hamsters were captured by the method of flooding their burrows (A n d r z e j e w s k i & G l i w i c z, 1969). A water-cart, 2000 l in capacity, pulled by a tractor, was usually applied for this purpose. A total of about 450 hamsters were captured over the study period.

The age of animals (n = 85) was determined on the basis of their body weights and the weight of eye lenses fixed in 10% formalin and dried up by L o r d's method (1959).

The 24-hour activity of hamsters was studied by recording the number of passes of hamsters coming into and going out of the burrow, thereby interrupting a beam of infra-red light (W e i n e r & G ó r e c k i, 1974). This investigation was carried out in summer and autumn for two years (1973—1974). Altogether, activity was recorded in 153 days and nights.

During the period of 1971—1974 meteorological data were recorded in the station situated in the field where the hamster population was studied. Temperature was measured 2 m above, 50 cm below and at the surface of the ground. Rainfall was also noted.

In laboratory experiments the average daily metabolic rate (ADMR) was measured at 15 and 20°C by the consumption of oxygen, using a closed-system Morrison respirometer (M o r r i s o n & G r o d z i ń s k i, 1975). Animals were placed in 20-litre chambers and given nest material, food (grain, carrots, beets) and water ad lib. These measurements were taken on 66 hamsters, more than half of this number in winter and the remainder in summer.

The energetic cost of thermoregulation was established on the basis of the resting metabolic rate (RMR) measured at ambient temperatures from −12 to +35°C (G ó r e c k i & W o ł e k, 1975), using a Kalabukhov-Skvortsov respirometer (G ó r e c k i, 1975) and 10-litre respiration chamber. A total of 210 one-hour oxygen consumption measurements were made on 30 hamsters.

In order to determine the calorific equivalent of oxygen, the amounts of oxygen consumed and carbon dioxide breathed out were measured in a paramagnetic open-system respirometer (Spirolyt II). Measurements were taken at 15 and 20°C at a flow of 20 l/hr. In this way RQ was established in 14 hamsters.

Changes in the deep body temperature of hamsters caused by changes in ambient temperature were measured in 5 animals, after transmitters had been surgically placed in their body cavities (W e i n e r & G ó r e c k i, 1975). Body temperature was thus measured in a continuous way in hamsters exposed to 10 and 20°C. Three hamsters were exposed to 10°C for 13 days and two animals were exposed to 20°C for 10 days.

III. RESULTS

3.1. Number of Trappable Hamsters

In the annual cycle the total number of hamsters was determined by three factors: the natural mortality of hamsters, the appearance of juveniles in the fields and the migration of these animals from one field to another. Such migrations, usually caused by agrotechnical procedures, brought about enormous changes in the number of hamsters. E.g., in the second half of August in 1973 there were 11 hamsters per hectare in a field of lucerne and a week later, after the field had been ploughed, this value decreased to less than 4 hamsters/ha, while in the adjacent

fields, already sown with wheat and rape, and in the field from which maize had not been gathered yet, their number increased conspicuously. The autumn of 1973 was rather dry, the rainfall being scarcely 19 mm in the period from mid-August till mid-September; this is why, after the field of lucerne had been ploughed, practically nothing was left to eat and the animals, especially those which had their burrows in the middle of the field, had to move to neighbouring fields.

The number of burrows falling to one hamster averaged 4.43 for all the years of this study, being lowest in 1974, when the number of hamsters was highest (3.75 burrows in the spring and 3.90 in the autumn). The highest numbers of burrows were recorded in 1972, the mean for this year being 5.05.

In spite of the fact that at each estimation the burrows were counted in an area averaging 2.0 to 7.5% of the whole field of a given crop, the

Table 1

Number of burrows determined in fields with different crops in the autumn 1974.

Field	Area, ha	No. of deter-mination	Examined part of the field, %	Number of burrows		
				Transect 750 m² ± ± SD	C.v., %	ha
Lucerne [1]	22	10	3.4	7.30 ± 3.05	41.7	97.3
Wheat [1]	24	8	2.5	6.75 ± 1.31	19.4	90.0
Vicia faba [1]	23	6	2.0	7.33 ± 3.07	41.8	97.7
Maize	36	10	2.1	4.10 ± 1.03	25.2	47.3
Potatoes	10	5	3.8	1.40 ± 1.14	81.4	18.7
Pape	12	6	3.7	1.75 ± 1.16	66.8	23.3
Grasses	1	4	30.0	3.25 ± 0.96	29.5	43.3

[3] Stubble

differences between the estimates were rather remarkable — the coefficient of variation often exceeded 40%. In the fields with perennial crops (grasses, clover, lucerne), where the burrows were distributed least uniformly, their number was usually estimated over larger areas. The transects in which the burrows were counted extended obliquely across the whole field, but the number of burrows did not, as a rule, depend upon the distance from its edge. The fields of rape, the peripheries of which more abounded in burrows than the centres, were the only exception. A similar phenomenon was observed in a field of potatoes in 1974. The results of the number estimation made in the autumn of 1974 are given in Table 1.

In each year of study the number of hamsters was distinctly higher in autumn than in spring (Fig. 2). The highest number was observed in the autumn of 1974 when there were about 2150 hamsters in the whole study

area (128 ha) or 16.8/ha. In the spring 1973 the lowest number of only
3.9 hamsters/ha was noted.

In 1972—1974 the mean annual numbers of hamsters per ha calculated by
the method proposed by P e t r u s e w i c z & M c F a d y e n (1967) were,
8.4, 7.8 and 9.3 hamsters respectively. These figures do not include
the juveniles that appeared in the fields early in the summer, between
the censuses. On the basis of the data concerning the number of
embryos the number of young animals was estimated and next taken into
account in the calculation of the flow of energy through the whole popu-
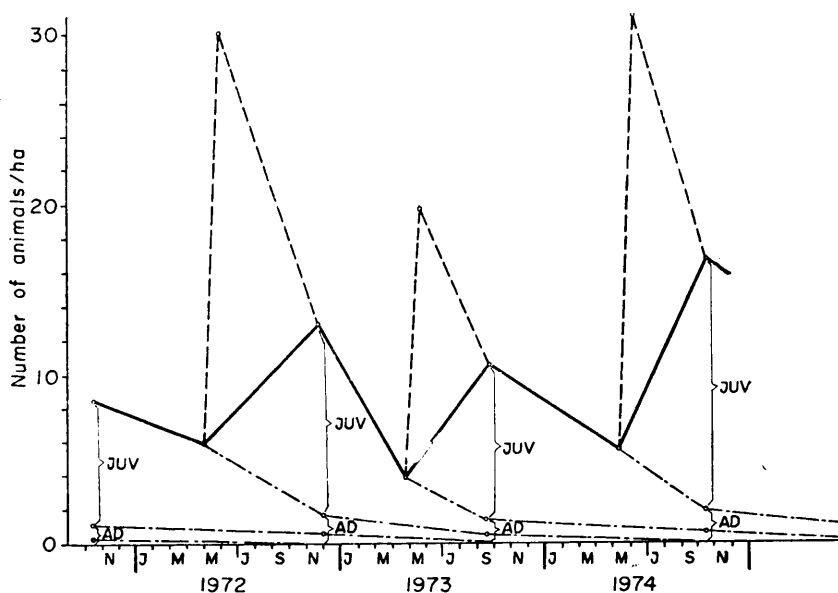lation (see also Section 3.5.).

Fig. 2. Dynamics of the number of hamsters.
Solid line — number of animals observed in the field, broken line — number of
young determined on the basis of the number of embryos, Juv — young hamsters,
Ad — one-year-old and older hamsters.

3.2. Sex Structure and Reproduction Rate in Hamster Population

3.2.1. Sex Structure

Each year the sex ratio in the population under study was estimated
on animals captured in the fields neighbouring upon those in which their
number was determined (Fig. 1, Field No. 3). Sex was determined in all
the animals captured except juveniles designed for laboratory studies.
As the number of animals captured in particular years was too small to
permit the determination of the sex structure of the population, the sin-
gular captures were summed up. Altogether 109 males and 119 females

were captured in 1971—1974. Since the difference between these num-
bers, examined by the chi square test, was not significant at the 0.05
confidence level, it was assumed for further considerations that, as in
most other rodent population, the sex ratio is 1 : 1.

3.2.2. Reproduction — Number of Young

A total of 25 pregnant females were captured from 20 May to 9 June in
two successive years. The average number of embryos per female
was 11.4. in 1972 and 9.9 in 1973. The mean number of embryos falling
to one pregnant female calculated for these two year was 10.3 ± 3.4 (S.D.).

Nestlings were found several times in captures (by flooding the bur-
rows), but their number never exceeded 8 specimens and their mean
number from 5 litters captured was 6.8 ± 1.6. Unfortunately, the small
number of young captured precludes any far-reaching conclusions,
especially since their number may have been underestimated because
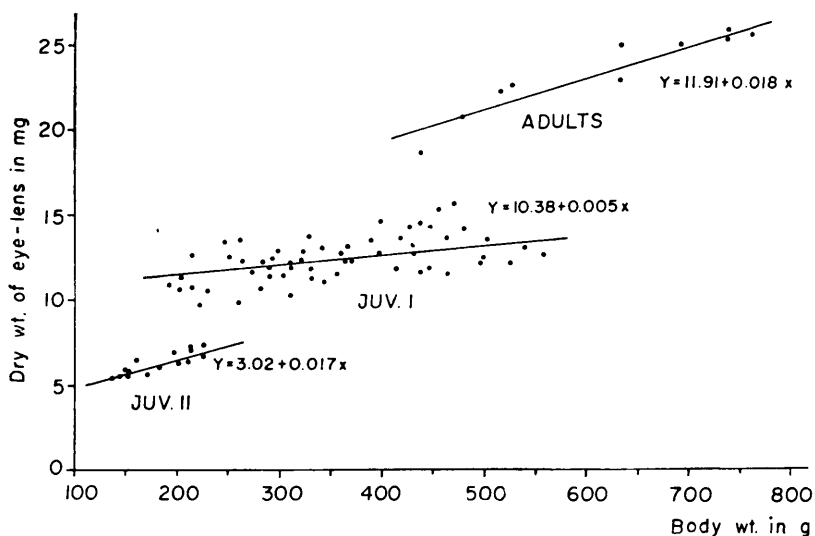not all of the young left their flooded burrows.

Fig. 3. Relationship between body weight (X) and dry eye-lens weight (Y), dif-
ferentiating the population into three cohorts.

3.3. Age Structure of Population

Forty-eight hamsters were captured in the autumn 1972 and 85 in the
autumn 1974. Captures were carried out in control fields (Fig. 1 — Field
No. 3), situated in the close vicinity of the fields in which the dynamics
of the number were being determined. In the first period (1971—1973),
however, only the body weights of animals caught were analysed, but
in 1974 the eye lenses were removed from the animal carcasses (L o r d,

1959) and on the basis of the weights of their dry matter the animals were divided into three age classes, for in the study period this was the only year in which the hamsters had two litters. The adult hamsters, aged one year or more, formed 11.8% of the population, the hamsters of the first litter 69.4% and those of the second liter 18.8%. In spite of differences in body weight between the hamsters (Fig. 3), the dry weights of eye lenses of the hamsters of the first litter lay within narrow limits of 0.0105—0.0140 g and were sharply demarcated from the weights of lenses

Table 2

Differentiation of body weight and eye-lens weight in three cohorts of autumnal hamster population in 1974.

	Adults	Youngs of the I litter	Youngs of the II litter
Body wt. g ± SE; C.v. %	618.6 ± 37.3; 19.3	348.1 ± 12.5; 27.6	185.1 ± 7.7; 16.6
Eye-lens wt. mg ± SE; C.v. %	23.3 ± 0.74; 10.0	12.3 ± 0.14; 8.9	6.2 ± 0.16; 10.2
Coefficient of correlation	0.941	0.484	0.835
Relationship between body wt. (X) and lens wt. (Y)	$Y = 11.91 + 0.018\,X$	$Y = 10.38 + 0.0005\,X$	$Y = 3.02 + 0.017\,X$
Significance of regression coefficient	$p < 0.001$	$p < 0.001$	$p < 0.001$

Table 3

Distribution of hamster of the population (number of animals per hectar) according to age.

Date	Adults, 1 year	Adults, 2 years (or more)	Youngs	Total
1971	0.80	0.34	7.36	8.5
1972	1.21	0.52	11.17	12.9
1973	0.99	0.43	9.18	10.6
1974	1.39	0.59	14.82	16.8

of the hamsters of the second litter and the adult ones (Fig. 3, Table 2). The differences in lens weight between all the three classes were examined by the t test and appeared to be very significant ($p < 0.001$) in all cases.

The dry eye lenses of the two biggest hamsters (860 and 800 g), captured in the spring 1974, were also weighed, their weights being, respectively, 0.0278 and 0.0255 g. The molar teeth of these animals were much more heavily worn than in several adult hamsters more than 450 g in weight and their cranial sutures were ossfied to a distinctly higher

degree. This points to the fact that the class of adult hamsters contained both one-year-old and older specimens. The class of adult hamsters was divided on the basis of body weight into two subclasses (limit weight — 600 g), whereas all the young animals were treated together. The results are illustrated in Table 3.

3.4. Body Weight and Growth of Hamsters

In 1974 the young hamsters of the second litter were captured at the age of 9 weeks and their weight at that time was about 185 g (Table 2). The young of the first litter were 27 weeks old at the time of capture and weighed 348.1 g.
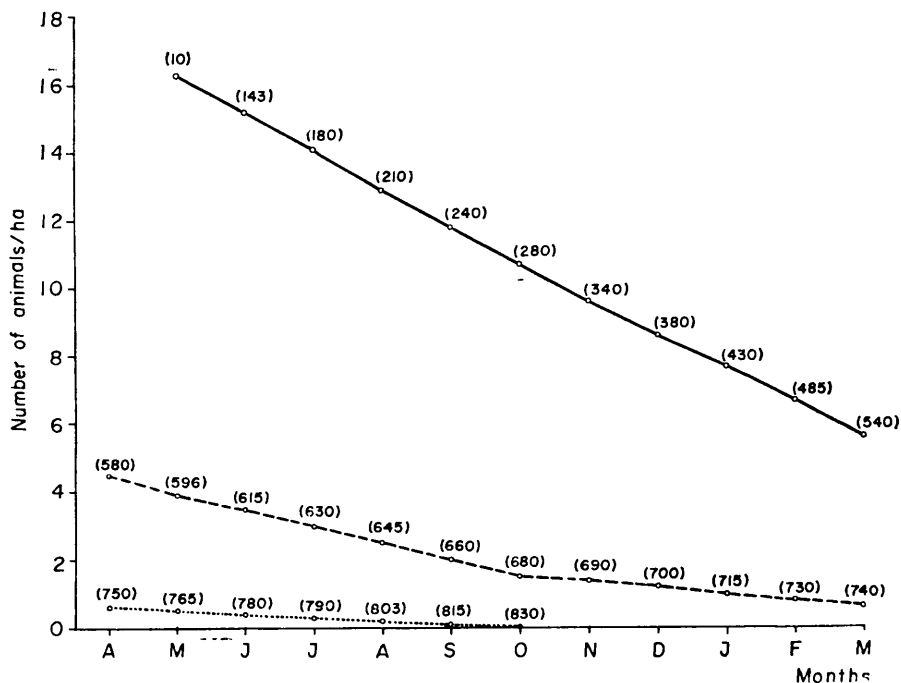

Fig. 4. Density of hamsters and their mean body weights in particular months of the year.
Solid line — young animals up to a year of age, broken line — hamsters up to two years of age, dotted line — 2—3-year-old hamsters; in brackets — body weights.

The mean body weight of the »spring« population of hamsters was 422.9 ± 85.3 g (n = 87 animals). On the other hand, 161 hamsters weighed in autumn were on the average lighter (319.8 ± 71.1 g), which naturally was connected with the presence of a large number of juveniles in the sample. The mean body weight was determined on the basis of the age structure of the specimens examined, their density (Fig. 4) and growth

curve. The mean annual body weight is 371.2 ± 139.6 g; an average ham-
ster reaches its highest weight in April, whereas in May, when the whole
growth of young still proceeds at the cost of females, the mean weight
is lowest and amounts to 132.9 g (Figs. 2 and 4).

Both the foregoing results and the data given by M o h r et al. (1973)
about the period directly following birth made it possible to establish the
dependence of body weight upon age in a hamster population over the
period of a whole year (Fig. 4).

3.5. Dynamics of Population Size

The number of trappable hamsters was determined in the field in
spring and in autumn. The peak of abundance occurred, however, in
summer months, starting from the end of May, when the juveniles began
to leave the nests.

The maximum number of hamsters in the fields (Fig. 2) can easily be
calculated from the previously established number of embryos falling to
one female (10.3 embryos — Section 3.2.2.) and the number of females
in the spring population (50⁰/o females, of which above 80⁰/o reproductive
— F r e n c h, S t o d d a r t & B o b e k, 1975). This high number soon
undergoes a reduction, since the highest mortality rate is observed in
rodents just after the young have left the nests (G l i w i c z et al., 1968;
P e t r u s e w i c z, 1970; P e t r u s e w i c z & H a n s s o n, 1975).

Having assumed the mortality at a level of about 42⁰/o in summer and
58.5⁰/o in autumn (cf. Section 3.6.), we were able to calculate the number
of hamsters in particular months (Fig. 2 and 4) and their mean annual
number. Such a very general mean number for the years 1971—1974 is
12.3 ± 5.1 hamsters/ha. The highest density occurs in June, when juve-
niles appear in fields (19.1/ha — Fig. 2 and 4).

3.6. Mortality, Survival Table

Most of the important population parameters, such as the turn-over of
number and biomass and the production of a population, demand the
knowledge of the survival table. In order to construct it, it is necessary to
estimate the probability for hamsters to live till a definite age. The
autumn numbers juveniles, one-year-olds, two-year-olds, and older indi-
viduals are compared in Table 4, which makes it possible to investigate
the fate of particular cohorts of animals. The division into one- and two-
year-old adult specimens was made on the basis of the data obtained in
the autumn seasons of 1973 and 1974, when about 30⁰/o of adult hamsters
were more than one-year-old. It was taken for granted that virtually all
hamsters die by the autumn of the third year.

The probability of one-year-long survival (p_1), from the first autumn to the second, is

$$p_1 = \frac{127+177}{1430+1175} = 0.117 \tag{1}$$

whereas the probability of survival throughout the period from the second autumn to the third

$$p_2 = \frac{55+76}{127+155} = 0.465 \tag{2}$$

The probability of survival calculated in this way permits the construction of a life table with yearly age classes. Since on account of differences in physiology between hamsters in summer and in winter it is indispensable for further considerations to know the changes in the size if particular age classes in these seasons, the intervals had to be reduced to half-year

Table 4

Changes in the numbers of individuals
of particular cohorts in successive years.
Data based on autumnal estimates.

Age classes	Number of animals/128 ha		
	1972	1973	1974
Youngs	1430	1175	1897
Adults — age 1 year	155	127	177
Adults — age 2 years	66	55	76
Adults — age 3 years	0	0	0

ones. For this purpose the decrease in the number of adult hamsters was calculated for the period from the autumn 1973 to the autumn 1974, when the richest material was captured. In the period of active life the reduction of the number of these hamsters was 65.4% and thus it was higher than in the winter, when 46.2% of the hamsters perished. The probability of survival of the half-year period from spring to autumn (p_a) can therefore be computed from the equation

$$p_a = 1 - 0.654 = 0.346 \tag{3}$$

and from autumn to spring analogously

$$p_w = 1 - 0.462 = 0.538 \tag{4}$$

Probabilities p_a and p_w were calculated for an average hamster above half a year of age. The chances of hamsters to survive the period of active life and that of winter undoubtedly change with age. However, it was assumed that their mutual relation remains constant throughout their life and thus

$$p_a = 0.643 p_w \tag{5}$$

for all age classes. For hamsters in the first year of life $p_1 = p_w \times p_a = 0.117$. Substituting p_a from formula (5) in this equation, we obtained

the probability of survival of the first winter, which was 0.462, and the following summer, 0.275. Analogous reasoning was used for older hamsters and their probability of survival was calculated to be 0.849 for winter and 0.548 for summer. As can be seen, the chance to survive winter is better in the case of all hamsters.

Now, only the probability of survival of the period from birth to the first autumn (p_0) is needed for the construction of the survival table of hamsters. On account of the similarity of the mean numbers in successive years, it was assumed that the mean number of hamsters for many years is constant or that the measure of net reproduction, R_0, equals unity. This measure is defined by the formula

$$R_0 = \Sigma_x \, l_x \, f_x, \tag{6}$$

where l is the probability of survival till the age of x and f the number of female offspring falling to a female at the age of x (M c A r t h u r & C o n n e l l, 1966).

Table 5

Life table of hamster population.

x — age class in years, l_x — the number surviving at the beginning of age class x, d_x — the number dying during the age interval x, q_x — the rate of mortality, e_x — the expectation of life remaining for individuals of age x, f_x — number of female offspring born to a female in age x.

x	l_x	d_x	q_x	e_x	f_x
0.0—0.5	1000	630	63.0	0.56	0
0.5—1.0	370	212	57.3	0.60	0
1.0—1.5	158	115	72.8	0.56	5.15
1.5—2.0	43	6	13.9	0.91	0
2.0—2.5	37	17	45.9	0.52	5.15
2.5—3.0	20	20	100.0	0.25	0
3.0—3.5	0	0	—	0.00	0

In determining the value of f_x, it was assumed that the female produces its first litter in the spring of the year following the year of its birth or at the age of 1.0—1.5 years. As the second litter was observed only once during the five-year study of hamsters and even then it was much less numerous than the first litter, it was assumed for calculation that the female produces young only once a year, which situation was rather typical in the study region. It was also assumed that the sex ratio of the offspring is 1 : 1. According to the empirical data 10.3 embryos fall to one female or $f_x = 5.15$ (Table 5).

Successive values of l_x were substituted in formula (6) (Table 5), and p_0 was calculated to be 0.370. This value of p_0 makes it possible to calculate the probability of survival till the beginning of a given age interval (l), which in turn permits the computation of the mortality in the given

age class (d_x), the mean life expectancy ($\bar{t}$), and the turnover of the bio-mass (Θ) of these individuals. The mean life expectancy of hamsters was 0.564 year, *i.e.* nearly seven months, and the turnover of number 1.77.

3.7. Production of Population

In the study period the mean number of hamsters in the whole area of 128 ha was 660, half of which or 330 were females. If the number of females reproducing in spring is diminished by substracting from it the second litter from the previous autumn, which perhaps did not take part in reproduction then and besides does not often occur at all, about 88% or 291 females gave birth. The pregnant females of the whole study area therefore produced total of 2997.3 embryos. Even if the resorption of embryos was very high (up to 10% — P e l i á n, 1967, 1970), still
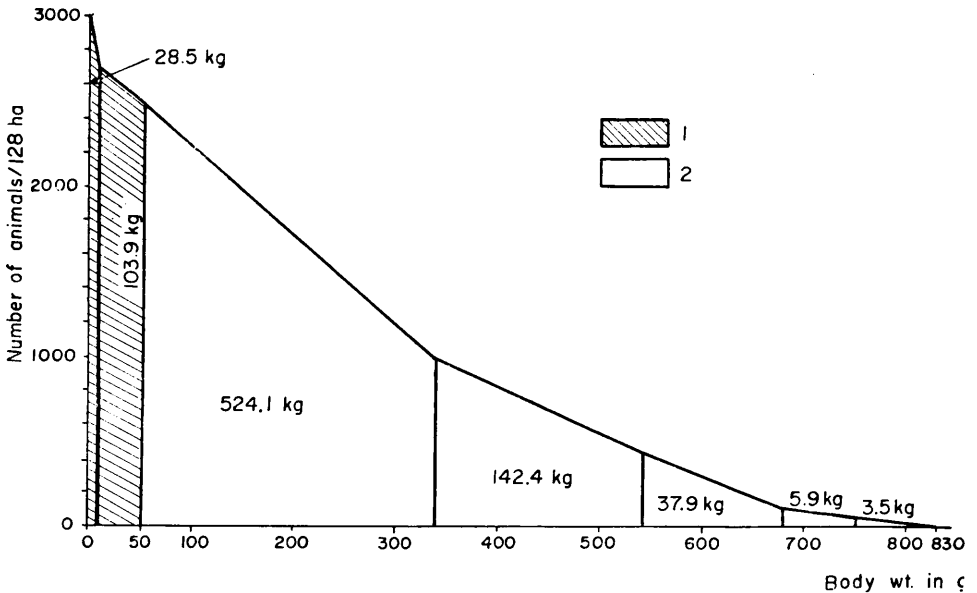

Fig. 5. Production of hamster population calculated on the basis of life tables. 1 — reproduction production (P_r), 2 — growth production (P_g). All values in kg/128 ha×yr.

2697.6 young hamsters were born, each of them weighing about 10 g (M o h r *et al.*, 1973; V o h r a l i k, 1975) (Fig. 5). Consequently, the production of embryos $P_E = [(2997.3 + 2697.6) : 2] \times 10$ g $= 28474.5$ g. At the 63% mortality, characteristic of that hime (Table 5), there were 998.1 half-year-old hamsters, approximating 340 g in body weight each (autumn data for the first litter). Thus the production at that time was 609.8 kg.

This value of production includes the production at the cost of the fe-male (lactation — P_L), which can be determined, if we know the body weight of the young ones that begin to feed by themselves. This weight

is however very hard to establish in a hamster population, because young animals begin to take supplementary food as early as the eighth day of life (K o w a l s k i. 1964), gradually replacing mother's milk with vegetable food. The body weight of hamsters that begin to feed by themselves was arbitrarily estimated at about 50 g. About 2500 juveniles left the nests (Fig. 5) and thus the production until this age was 103.9 kg. The total production due to reproduction (P_R) was 132.4 kg.

Since 42.7% of the population survived from the age of six months to the age of a year (Table 5) and the weight of a one-year-old hamster was about 540 g (data from autumn captures), the production in this half-year period was 142.4 kg. The production of hamsters in the next half-year (1.0—1.5 years old) was 37.9 kg, the calculation being based on the body weight, 680 g, of 7 hamsters captured in the autumn; the age of these animals was determined on the basis of the weight of their eye lenses and the wear of teeth, estimated by comparing them with the teeth of juveniles weighing about 300 g. The weight of 750 g was assumed for the next class, because this value was attained by the oldest specimens in which the age was determined. Here the production was 5.9 kg. Lastly, the weight of the two biggest hamsters captured during this study was assumed for the remaining specimens (Fig. 5). It was 830 g and then the production was 3.5 kg.

The production over the whole life of hamsters in the whole study area of 128 ha reached 828.1 kg or about 6.5 kg/ha. The production due to reproduction (P_R) was 1.03 kg/ha and that due to growth (P_G) 5.43 kg/ha. In most rodent populations the production due to reproduction form at least a half of the total production, whereas in hamsters it constitutes hardly 16% (P e t r u s e w i c z & H a n s s o n, 1975).

The turnover of biomass (Θ_B) can be calculated retrogressively from the foregoing data and the number of individuals (P e t r u s e w i c z, 1966, 1967; P e t r u s e w i c z & M c F a d y e n, 1970):

$$\Theta_B = P_N : B \qquad (7)$$

where P_N is the net production and $\bar{B}$ the mean biomass ($N_b \times B_b$).

The mean number (including young animals) in three consecutive years, 1972—1974, was 12.4 hamsters/ha and the mean annual body weight in the population was 371.3 g. The substitution of these values gives the turnover of biomass (Θ_B) equal to 1.40. This value is therefore lower than the turnover of numbers (Θ_N) calculated previously. Thus the phenomenon of slight inferiority of the turnover of biomass to that of numbers, observed in rodent populations, occurred also here (P e t r u s e w i c z, 1966; P e t r u s e w i c z, A n d r z e j e w s k i, B u j a l s k a & G l i w i c z, 1968; B o b e k, 1973).

An identical turnover of biomass was computed for a population of

Proechimys, a rodent resembling the common hamster in size and living in the tropical rain forests of Panama (G l i w i c z, 1973). This turnover is however distinctly lower than, *e.g.* the turnover in the population of *Clethrionomys glareolus* (P e t r u s e w i c z *et al.* 1968).

3.8. Daily Activity Rhythm and Sums

The method used to determine the daily activity of hamsters permits measurements in natural environment without disturbing the natural activity pattern of these animals. The results from summer (from May to July) differ somewhat from the autumn one (August—October). In
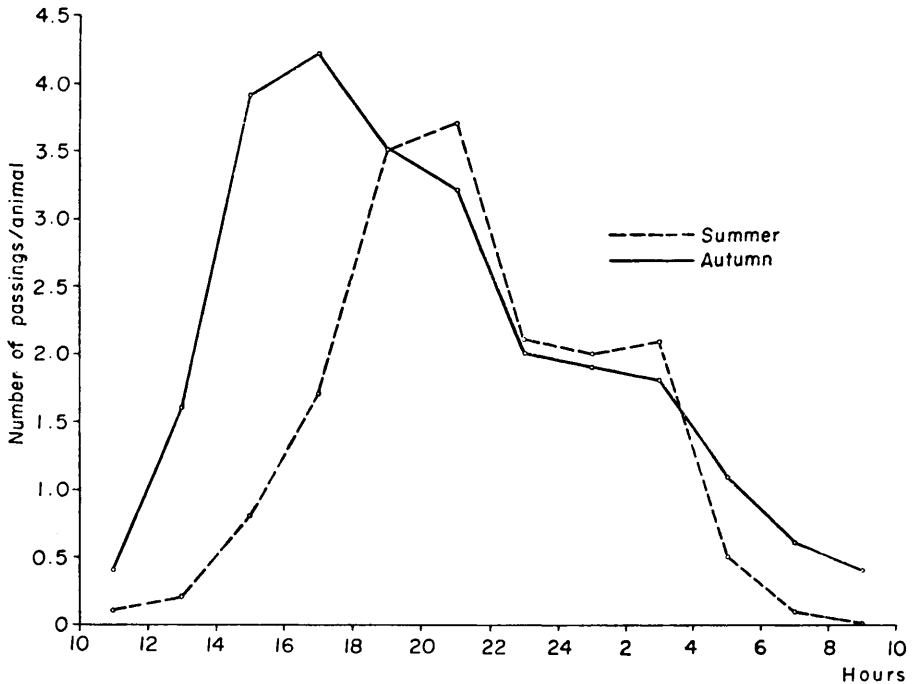

Fig. 6. Rhythm of daily activity of hamsters measured by the numbers of goings out of and comings into the burrow in summer and autumn.

summer the number of goings out of the burrow calculated for one hamster was 8.4. The activity rhythm (Fig. 6) had as a rule two peaks, the main peak about 8 p.m. and the lower one in the small hours of the day, from 0 to 2 a.m. In autumn the number of goings out of the burrow per hamster increased considerably, up to 12.3/day. The activity rhythm still had two peaks, but the main peak was shifted to earlier hours (4 to 6 *p.m.*) and was much wider at that (Fig. 6).

It was also found in sporadic observations made over the whole period of this study that the time of one stay of an animal out of the burrow

was shorter in summer than in autumn. If in summer such a stay did not exceed 20—25 minutes, in autumn a stay often exceeded 30—35 minutes. Often some individuals were observed in the fields (*e.g.* those of maize) as far as several hundred metres from their burrows, and it was just in such cases that the time of their stay out of the burrow exceeded 35 minutes.

Since in summer one hamster left its burrow on the average 8.4 times a day, the time of its stay on the ground was about 3.5 hrs per day, compared with 6—7 hrs per day in autumn.

3.9. Average Daily Metabolic Rate (ADMR) of Hamsters and Their

Body Temperature

ADMR of hamsters was studied at two ambient temperatures, 15 and 20°C. The body weights of animals examined differed rather much and ranged from 234 to 629 g at 15°C and from 187 to 629 g at 20°C, which permitted the calculation of the relationship between metabolism and body weight (Fig. 7). The regression equations and coefficients of cor-
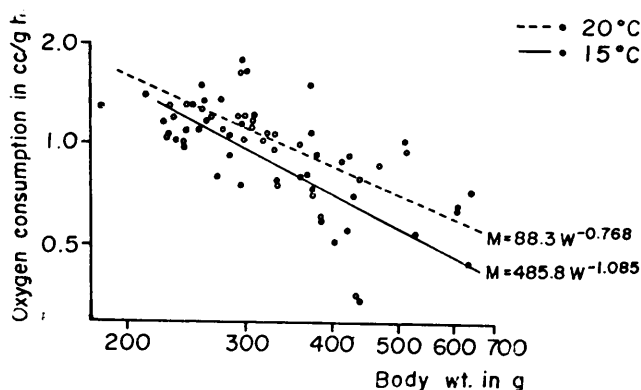

Fig. 7. Relationship between the mean daily metabolic rate of hamsters (*M*) at 15 and 20°C and their body weight. Double-log scale.

relation and regression (Table 6) indicate that the dependence of the metabolic rate upon the body weight was very highly significant.

The daily rhythm of metabolic rate (Fig. 8) showed an extreme coincidence at the time of activity of these animals at both ambient temperatures applied. The peak of this activity occurred at night, between 10 and 12 *p.m.* There was however a slight difference at time of their minimum activity and then the metabolism measured at 15°C was somewhat lower than at 20°C (Fig. 8). This result influenced the total result so that *ADMR* at 15°C was lower than at 20°C by about 15%. At both temperatures the maximum metabolic rate was on

the average 2.11 times as high as the minimum one, which was 0.69 cc O_2/g hr. The consumption of oxygen in night hours was 1.36 times as high as in the day-time.

Table 6

Average daily metabolic rate (*ADMR*) of hamsters measured at ambient temperatures 15 and 20°C and its dependence upon body weight.

ADMR (cc O_2/g hr ± SE)	1.00 ± 0.07 (at 15°C)	1.08 ± 0.05 (at 20°C)	1.04 (average)
Max *DMR*	1.46	1.44	1.45
Max/Min *DMR* ratio	2.3	1.9	2.1
Night/Day ratio	1.51	1.26	1.36
Body weight, g ± SE	334.0 ± 19.6	347.1 ± 16.9	341.7
ADMR (*M*) and body wt. (*W*) correlation coefficient	−0.708 0.02 < p < 0.05	−0.602 0.01 < p < 0.02	−0.642
Regression equation	$M = 485.8\,W^{-1.085}$ $p < 0.001$	$M = 88.3\,W^{-0.768}$ $p < 0.001$	$M = 162.9\,W^{-0.883}$ $p < 0.001$

Most *ADMR* measurements were made in the winter (on animals captured late in the autumn), at the time when hamsters hibernate under natural conditions. It appeared however that the results obtained in the winter did not differ significantly ($p < 0.05$) from the summer results.

Fig. 8. Daily metabolic rhythm of hamsters at two ambient temperatures. The thickened line of the *x*-axis represents night-time.

The differences in body weight between two groups were at the border-level of statistical significance ($p = 0.05$). Consequently, the results obtained both in the summer and in the winter could be analysed together (Table 6).

The metabolic rates of hamsters measured at 15 and 20°C did not differ significantly ($p < 0.02$), neither did the body weights of hamsters

differ between the two groups ($p<0.01$). Thus, the metabolic rates at 15 and 20°C could be pooled together to calculate the common dependence of *ADMR* upon body weight for both ambient temperatures: *ADMR* (cc O_2/g day)$=7.05\ W^{-0.883}$. This equation was used later as the basis for construction of the daily energy budgets of hamsters.

The measurements of *ADMR* were carried out for several days (above 75 hours) at both ambient temperatures. They were made for 10 hamsters at 20°C and for 6 at 15°C. The mean body weight of the hamsters used at 20°C was 425 g and at 15° C 408 g. The oxygen consumption in the first day was rather high and amounted to 1.11 cc/g hr at 20°C and 0.94 at 15°C (Fig. 9). It the following days *ADMR* decreased distinctly and the differences between consecutive days were not significant (p always below 0.05). At 15°C it was 0.69 and at 20°C 0.87 cc/g hr, retaining a similar daily rhythm. The results seemed to indicate a fall in the body
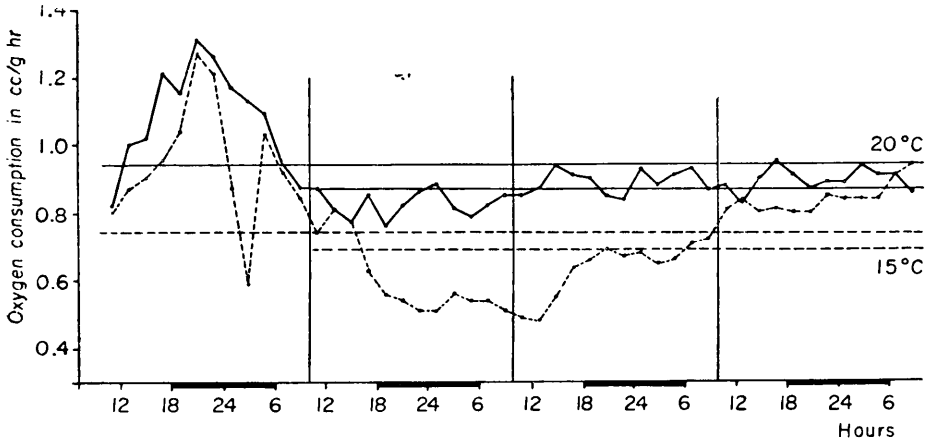

Fig. 9. Rhythm of *ADMR* of hamsters measured at 15 and 20°C during an uninterrupted four-day experiment.
Thickened line of x-axis — night-time, longer, solid and broken, straight lines — *ADMR* for the whole period of measurements, shorter lines — *ADMR* for three days.

temperature of hamsters during these measurements, which however was not confirmed by the continuous telemetric measurements of deep body temperature on animals exposed to 10 and 20°C. These measurements were made on 5 hamsters over a period of 4—7 days (Fig. 10).

In the course of the days of exposure the body temperature of the hamsters did not change in an essential manner; as indicated by the range of variation, it did not show a tendency towards either direction of changes. Both at 10 and at 20°C the body temperatures of hamsters were very similar and lay within narrow limits of 37—38°C (Fig. 10). The rhythm of changes at both ambient temperatures was similar; the

highest values were noted in the afternoon, but the differences were
small and did not exceed 0.5°C. The very interesting problem of rela-
tionship between metabolism and body temperature in hamsters seems
to need further studies.

3.10. Chemical Thermoregulation

The production of heat for the maintenance of stable body temperature
was determined by the consumption of oxygen within a range of ambient
temperatures from — 12 to +35° (G ó r e c k i & W o ł e k, 1975).
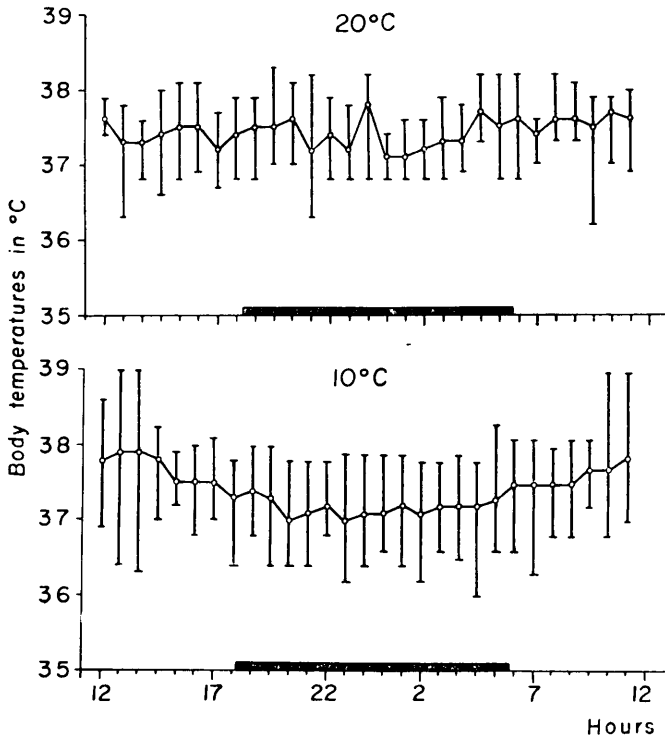
Fig. 10. Daily fluctuations of deep body temperature of hamsters exposed to 10
and 20°C. Mean values and ranges of variation are given.

The dependence of metabolism (M) upon ambient temperature (T)
at physiologically low temperatures is defined by the equation

$$M \text{ (cc } O_2/g \text{ hr)} = 1.97 - 0.07 \, T \tag{8}$$

The intensity of heat production for thermoregulation is $5.33\%/°C$
within a range of T_a from -12 to $+27.5°C$ and $4.44\%/°C$ within a range
from 20 to 0°C and then it is very high as for an animal of so great
a body weight.

3.11. Respiratory Quotient (RQ)

In order to determine the calorific equivalent of oxygen the amounts of O_2 consumed and CO_2 produced at that time were measured in a paramagnetic respirometer. Before measurement the animals were given a mixed diet, the same as was applied during measurement of *ADMR* and *RMR*.

RQ measured at 20°C in 9 hamsters averaged $0.72 \pm$ (SE) 0.02 and at 15°C in 5 hamsters it was nearly the same (0.71 ± 0.03). As these values do not differ significantly both results were treated together. The calorific equivalent of oxygen was to be assumed 4.7 kcal/l O_2 (acc. to K l e i b e r, 1961).

3.12. Food Storage

In the autumn of 1973 and 1974 16 burrows were excavated to investigate the winter food supplies of hamsters. Although the excavated burrows were inhabited by hamsters (in two cases the animal was caught in the burrow) and the course of the passages of the burrows had been marked with coloured water prior to excavation, we failed to dig out the stored provisions. In two burrows we found 0.8 and 1.4 kg of corn and maize grain, but they were shallow burrows without chambers and ramifications and were used as temporary hiding places and not as main residential ones.

Because of the failure in determination of the magnitude of supplies a direct attempt was made to find them by computing how much food hamsters bring to their burrows. Maize grain from the cheekpouches of two hamsters (body weight about 350 g), captured while they were carrying food, was weighed. A hamster appeared to carry 9.5 g of dry matter of grain at a time. Maize ripened ununiformly in the field so that the hamsters were able to gather ripe seeds and carry them to the burrows for 3 to 5 weeks. On the assumption that each departure from the burrow was combined with gathering food, a relatively small hamster, leaving the burrow 12.3 times a day (see Section 3.5.), was ables to store about 117 g of grain daily. This makes about 2.9 kg of grain of maize only during the period of 3—4 weeks.

As can be seen from field observations, hamsters store their supplies for about 90 days, from August to October. In this period a relatively small hamster can store a maximum of about 10.5 kg of dry matter of grain. Within the same time a larger animal can probably store larger amounts of food. However, the amount exceeding 15—20kg, given by some authors (e.g. W a l k e r, 1964), seem rather doubtful.

A. Górecki

3.13. Bioclimate

In addition to the many-year data, the air temperatures in the hours of maximum activity of hamsters were calculated for the four-year period of study (1971—1974) on the basis of the records of thermographs so that they might be used in computing the daily energy budget of the hamster population under study. The highest activity of these animals fell on the average between 3 and 11 *p.m.* in the period of summer and autumn (see Section 3.8.). These temperatures were next used to calculate the energy cost of the out-of-nest activity of hamsters. As can be seen, the temperatures at the time of maximum activity differ rather considerably from the mean daily air temperatures at a height of 2 m (Table 7). The last column of the table presents the temperatures at

Table 7

Some climatic parameters of study area.

Months	1949—1971		Temperatures:			
	Air tempt., °C (2m)	Rainfall, mm	Ground surface [1]	Depth 50 cm [1]	During max. activity of hamsters	Depth 160 cm [2]
January	−3.7	26.0	—	0.3	—	3.4
February	−2.7	24.2	−1.9	0.3	—	3.0
March	1.3	26.8	−3.6	2.0	—	2.6
April	8.4	32.0	0.9	7.0	—	2.3
May	13.4	57.3	5.6	11.9	8.9 ⎫	—
June	17.1	75.2	8.7	15.7	14.4 ⎬ 13.9[3]	—
July	18.4	95.3	11.5	18.0	17.2 ⎪	—
August	17.8	66.1	9.2	18.3	15.2 ⎭	—
September	13.8	46.0	5.5	15.0	11.9 ⎫	—
October	8.7	31.8	0.1	9.5	5.4 ⎬ 7.2[3]	—
November	3.7	40.2	−2.9	4.4	3.9 ⎭	6.0
December	−0.3	36.1	−7.0	0.4	—	4.4
Annual mean/sum	8.0	557.0	5.2			

[1] 1972—1974; [2] Accounted from M o l g a, 1958; with snow cover; [3] Average.

a depth of 1.6 m (converted acc. to M o l g a, 1958), taking into account the effect of snow cover (F o r m o z o w, 1946), for hamsters' nest chambers are usually situated at this depth in winter. On the basis of empirical data obtained by M o l g a (*l.c.*) the temperature at a depth of 1.6 m in the soil, with or without snow cover was raised by 40—80% in successive months of winter. These temperatures were used to calculate the costs of the activity of hamsters during the pauses in hibernation.

IV. DISCUSSION

4.1. Dynamics of Number

The determination of the actual number of hamsters was possible only after making several assumptions. It was thus assumed that only one hamster as a rule inhabits a burrow, further that about 20% of

females take part in reproduction and that a female gives birth to only one litter yearly. Lastly, several demographic parameters concerning the population under study were also assumed. Then, it was necessary to compare the views of different authors on these assumptions and, if possible, to find if they were relevant to the population being examined.

There is an extensive paper on the demographic parameters of various mammalian species published by F r e n c h, S t o d d a r t & B o b e k (1975), but none of the values given in it refers to hamsters. The mean values specified for the whole group *Cricetinae* may however be compared with the results obtained and assumptions made in the present paper. Naturally, such a comparison can be only very general, since these mean values for the whole family *Cricetidae* were calculated from rather considerably varying parameters for concrete species, obtained under very various climatic conditions.

All the estimates of the number were based on the assumption that except for the breeding season hamsters live singly in their burrows. In literature only one author (S t r o g a n o v a, 1954) states the occurrence of several hamsters in one burrow, which however has not been confirmed by any other writer. P e t z s c h (1952) and P o p o v (1960) never found the presence of more than one hamster in a burrow. S a m o s (1975) writes even that always when two hamsters had been introduced into an artificial burrow, one of them was soon bitten to death. These facts were corroborated by the author's own observations. In the period of 5 years 450 hamsters were captured by the flooding method and always only one hamster left one burrow. Naturally, females with young were exceptions and then only during a short period of nursing. In the light of the foregoing data it seems that the assumption, which might have been the source of some errors, is congruous with the behaviour pattern of hamsters.

The density calculated in the present paper, as the most general mean from several years, was about 12 hamsters/ha and thus very similar to that given by F r e n c h, S t o d d a r t & B o b e k (1975), who, having juxtaposed the data obtained by different autors, demonstrated that in the *Cricetinae* the density fluctuates between 10 and 15 individuals/ha, according to season. However, there were distinct differences in some demographic parameters. The life expectancy calculated in the present study was 6.7 months, whereas its interspecific mean for the *Cricetinae* was 3.6 months. Similarly, the number of embryos, which can be calculated from the tables given by those authors, is clearly lower than that obtained for the *Cricetus* population (respecively, 5.8 and 10.3 embryos per female). In the hamster population the number of females taking part in reproduction, though only an estimate, seems to be higher

than its interspecific mean. The greatest difference is however that in the number of litters per year. In the population under study hamsters had the second litter only once in five years, whereas the above-mentioned authors write that the mean numbers of litters exceeded three per year for all the cricetine species that they had data for. A simil-ar number, this time exclusively for hamsters, is given by K o w a l s k i (1964), and W a l k e r (1964) writes about two litters yearly. The general interspecific mean value is naturally influenced by the higher numbers of litters in small members of this family.

Concluding this comparison, I venture the supposition that the picture of the dynamics of the number of hamsters presented in this paper is fairly true and does not deviate much from the changes which occur in the field.

4.2. Energetics of Hamster Population

4.2.1. Hibernation and Energy Sources in Winter

Under thermal conditions prevailing in the study area the hibernation season usually lasted for about 5 months or, if the outset of winter was early, for 5.5 months. The hamsters sank into the winter sleep from the end of October to mid-November and usually started their active life in mid-April. In the winter hamsters have at their disposal two sources of energy, fat substances deposited in their body and food supplies stored in the autumn.

K a y s e r (1961, 1971) observed several hamsters over the five-month period of hibernation at 7°C under laboratory conditions. In these animals he examined the length of the period of uninterrupted sleep, charges in body weight, and fat content. In October and November the animals hibernated continuously 63 and 78⁰/o of the time and during these months their body weight decreased by 13⁰/o. In December and January the hamsters »slept« on the average half the time, their body weght increased somewhat at first and then dropped by nearly 17⁰/o. The maximum decrease in the body weight of hamsters averaged 1)⁰/o. During the last two months the percentage of »sleep« diminished on the average to 30⁰/o and the weight of hamsters increased slowly to reach the autumnal level.

These observation show clearly that in the first part of the winter hamsters wake up for a very short time and avail themselves chiefly of substances deposited in their body and relatively little of supplies stored in the burrows. In the second half of the winter, when the energy stored in their body has already run out, hamsters begin to complement it by eating intensely, as indicated by the shortened »sleeping« periods and the increase in their body weight.

According to J a g o s z (unpubl. data) in *Microtus arvalis* the amount of energy obtained from the combustion of a gram of own tissues is about 6 kcal. Similar values are given for large mammals and birds by K i n g & F a r n e r (1961) and B l a x t e r (1966). If these indices are adopted for hamsters, a 400 g animal obtains more than 450 kcal by the combustion of 19⁰/₀ of its own tissues (K a y s e r, *l.c.*) whereas the remaining amount of energy needed to survive the winter must be derived from food consumption.

The hamsters observed by K a y s e r (*l.c.*) began hibernation in October which ended it in February. Under the climatic conditions of the fields studied in the present work this period must be shifted by one month, since in October all the hamsters were still active and they distinctly higher. The consumption of oxygen by 370-gram hamsters observed by K a y s e r (*l.c.*), but shifted by a month, was therefore used to calculate the flow of energy through the hamster population (Table 8).

4.2.2. *ADMR* and Out-of-nest Activity

ADMR formed the basis for construction of the daily energy budget (*DEB*) (G r o d z i ń s k i & G ó r e c k i, 1967; H a n s s o n & G r o d z i ń- s k i, 1970; G r o d z i ń s k i & W u n d e r, 1975). The closed-system Mor- rison respirometer used in this study limited the size of the chambers in which an animal was placed during measurements. Although the hamsters were examined in large, 20-litre chambers containing nest material and food, their locomotor activity was restricted. It is then probable that the value of *ADMR* is somewhat underestimated. V i s i- n e s c u (1968) made similar measurements in four seasons but on a small number of animals. The daily metabolic rhythm obtained by this authoress much resembled that found in the present study, but the metabolism — unfortunately the measuring method was not given — was distinctly higher. The consumption of oxygen by 370-gram hamsters at 23°C was about 1.4 cc/g hr. Rectal temperature was measured in the same 12 hamsters, but as the measuring method was different, the temperature of these animals was naturally lower than that obtained in the present work.

Since the measurement of *ADMR* includes both sleep and rest periods and the activity periods, the costs of thermoregulation outside the nest chamber was added to its value for the time period during which the hamster was active. It was assumed in accordance with measurements that the body temperature in hamsters does not fall during the intervals between periods of hibernation.

The ambient temperature obtained for the winter was converted acc.

Table 8

Daily energy budget of hamster population.

Parameters of *DEB's*	Jan.	Febr.	March	April	May	Jane	July	Aug.	Sept.	Oct.	Nov.	Dec.	References
Duration of interruped sleep in % of month (f)	53.0	48.3	27.7	0	0	0	0	0	0	0	63.0	77.7	Kayser, 1961
Duration of activity in % of day (1-f-g)	6.3	6.3	6.3	15.0	17.0	20.0	25.0	27.0	30.0	30.0	6.3	6.3	This paper Molga, 1958
Ambient temperature in °C during activity	3.4	3.0	2.6	2.3	8.9	14.4	17.2	15.2	11.9	5.4	6.0	4.4	recalculated
Cost of reproduction kcal/day female in reproduction period	0	0	0	4.5	18.5	0	0	eventually 4.5	18.5	0	0	0	This paper
Average body wt in g	462.7	511.1	559.0	600.0	132.9 [1] 601.4 [2]	242.8	268.1	287.3	304.6	336.0	384.5	419.2	Mohr *et al* 1973. This paper
Density — animals/ha	8.7	7.5	6.3	6.1	20.8 [1] 5.3 [2]	19.1	17.4	15.6	13.9	12.2	11.0	9.8	This paper
DEB (kcal/animal day)	20.5	22.3	30.3	46.0	38.5	36.9	36.5	37.9	40.2	44.2	15.8	10.8	This paper
Respiration (kcal/ha day)	178.5	166.9	190.8	220.5	602.3	704.9	636.7	592.1	559.4	539.9	173.4	105.9	This paper

[1] All animals, [2] Adult animals

to M o l g a (1958) and the author's own data (Table 7). The nest chambers being situated at a depth of 1.2—2.0 m, as shown by field observations, so that the temperatures for the depth of 1.6 m were used for conversions, in which the effect of snow cover was also taken into account (F o r m o z o v, 1946). The mean temperature at the time of maximum activity was used to calculate the correction for thermoregulation in the summer (Table 7, Fig. 6). The costs of out-of-nest thermoregulation were estimated using the data concerning the animals' activity (Fig. 6), the equation of relationship between metabolism and temperature (Section 3.9) and also K a y s e r's (1959) data.

4.2.3. Energetics in the Period of Pregnancy and Lactation

The reproduction season (pregnancy and lactation) is particularly expensive as regards energy (K a c z m a r s k i, 1966; T r o j a n & W o j-c i e c h o w s k a, 1967; M i g u l a, 1969; G r o d z i ń s k i & W u n d e r, 1975). It has been assumed that over 80⁰/o of females take part in reproduction, which is not an exceptional proportion in cricetines (F r e n c h, S t o d d a r t & B o b e k, 1975), and calculated from the field data concerning reproduction and the data given by M o h r *et al.* (1973) that a female produces 93 g of embryos. The calorific values of such young rodents is about 1.1 kcal/g (G ó r e c k i, 1965). Consequently, the energetic value of the whole litter is 102.3 kcal. In order to produce such a number of young in 18—20 days of pregnancy, the female must additionally consume about 135 kcal. The mean assimilation coefficient assumed here for various foods is 76⁰/o (G ó r e c k i & G r y g i e l s k a, 1975). In order to spread this value uniformly over the period of month, 4.5 kcal/reproducing female or, more conveniently, 1.98 kcal/average individual of population must be added to the daily energy budget of each day of April, for this is when reproduction occurs.

The period of lactation, which in hamsters lasts for about 18 days (M o h r *et al., l.c.;* S a m o š, 1975) is much more expensive energetically. However, as early as the einghth day of life the young hamsters begin to take additional food, which gradually replaces the share of milk in their diet. It is therefore very difficult to establish to what degree mother's milk satisfies the energetic requirements during the growth of young. It has been assumed here that these animals increase their weight by 40 g (from 10 g to 50 g) from mother's milk alone. The calorific value of such hamsters has been assumed to be 1.25 kcal/g (G ó r e c k i, 1965). The energetic value of the growth is 465 kcal for the whole litter. All this energy comprised in milk must be produced by the female during the first, little more than ten days of lactation. Even if the efficiency of milk production reaches about 90⁰/o (M a y n a r d & L o o s l i,

1962) and the coefficient of assimilation of this food by young is similar,
a female must consume about 574 kcal extra during a dozen days or so.
Thus, 18.5 kcal must be added to the daily budget of each lactating
female for each day of May or 8.14 kcal/day to that of each animal
of the population. The respiration of young has been omitted in this
calculation, because their energy expenses are at the cost of mother's
milk.

Such extra daily energy expenditure is very considerable, the more so,
because it is much higher in the first several days of lactation. At that
time practically no high-energy foodstuffs occur in fields. It seems that
just at the time of reproduction females make use of the food supplies
gathered in the burrows and left uneaten after the winter. This is sup-
ported by the fact that the food stored markedly exceeds the total energy
expenditure in the winter and that in the course of the present study
remains of food supplies collected in the preceding year were found in
hamsters' burrows as late as the early summer. The utilization of
a portion of the supplies in the reproduction season may in part account
for the enormous effort these animals make to gather such an excessive
amount of food in the autumn.

4.2.4. Construction of Daily Energy Budget (DEB)

As can be seen from the preceding considerations, *DEB* of the hamster
consists of several components:

(1) fraction of hibernation (f) — naturally only in winter months;
in order to avoid computing the dissipation of energy over a whole
month, but only that in an average day, it was assumed for simplification
that the percentage of sleep is identical in each day of a given month
(Table 8);

(2) stay of animal in the nest (g), the basis for which was *ADMR*
at 20°C (D a n i e l, 1964; G r o d z i ń s k i & G ó r e c k i, 1967; G ó-
r e c k i, 1968; H a n s s o n & G r o d z i ń s k i, 1970);

(3) thermoregulation out of nest (activity) $1—f—g$. It was assumed
that in the winter, when the hamster stays in the burrow all day, it is
absent from the nest chamber for only about 1.5 hours (*i.e.* 6.25% of
the day). A very drastic reduction of the time of activity in the winter
was observed in many rodents (S a i n t   G i r o n s, 1966; G r o d z i ń-
s k i   &   G ó r e c k i, 1967). During this short time of true activity,
e.g. feeding in the store-chamber, thermoregulation was computed on
the basis of the actual soil temperature at a depth of 1.6 m (Tables 7
and 8).

Hibernation was calculated from the equation of relationship between
metabolism at the time of this process and body weight given by

K a y s e r (1959, 1961) and the fraction (f) of continuous »sleep«
(Table 8). In its final form this part of the budget was

$$M \text{ (kcal/g day)} = 0.002\, f\, (W : 1000)^{-0.06} \tag{9}$$

On the other hand, the dissipation of energy at the time of active life
was calculated on the basis of relation

$$M \text{ (kcal/g day)} = 18.38\, W^{-0.883} \tag{10}$$

The exponent b in the equation of relationship between *ADMR* and
body weight obtained in the present study differed statistically highly
significantly ($t = 2.9$, $0.01 < p < 0.005$) from the exponent (0.5) found in
very many rodents (H a n s s o n & G r o d z i ń s k i, 1970; G r o d z i ń-
s k i & F r e n c h, 1974). *DEB* was therefore calculated on the basis
of the unconverted relationship of *ADMR* and body weight obtained
in this work.

The correction for thermoregulation out of nest (at the time $1-f-g$)
was introduced into equation (2). Since the intensity of production of
heat for thermoregulation was determined to be 5.33%/°C (Section 3.10.),
its multiplication by the time of out-of-nest stay and ambient tempera-
ture (t) express the respiration during active life

$$M \text{ (kcal/g day)} = 18.38\, W^{-0.883}\, [g + (1-f-g)\,(2-0.05\,t)] \tag{11}$$

The correction for thermoregulation out of nest (at the time $1-f-g$)
correction for reproduction. Naturally, this correction concerns only two
months (May and June), if the population has one litter yearly, or four
months (in addition, August and September), if there are two litters
(Table 8).

In particular months of the year the two components of the budget
(equations 9 and 10) are added together in appropriate proportions to
receive the dissipation of energy expressed as the respiration of the
animal. The respiration of an average animal of the population during
a year was obtained by substituting in this expression the mean body
weights from the hamsters actually occurring in the study area in
successive months (Table 8, Fig. 4) (C a n g u i l h e m & M a r x, 1973).

The costs of maintenance of an individual thus calculated are lowest
in November and December, because the animals »sleep« for a large
part of the time (Table 8). The highest respiration is observed in April
(46 kcal/g day), mainly because the weight of hamsters is very high and
an additional amount of energy connected with reproduction is added
to the budget. Despite lactation, in May *DEB* is only 38.5 kcal/g day,
because lactation lasts relatively short and the mean value for this
month is greatly influenced by the energy budgets of juveniles, whose
body weight is low.

In order to obtain the value of the respiration of the whole population
during the year, the indivdiual budgets of average hamsters of given

months were multiplied by the density of hamsters in the study area at that time (Table 8, Figs 2 and 4). The energy requirement of hamsters increases from March to June and then begins to decrease in connection with a fall in the density of the population (Fig. 11). The lowest energy requirement naturally occurs in the winter months, when the hamsters hibernate continuously for about 70% of the time (Table 8, Fig. 11).

The total yearly respiration of the hamster population is 1.444×10^5 kcal/ha, of which 2.461×10^4 kcal/ha falls to 5 months with hibernation, or in the period active life this population dissipates about 83% of energy for respiration.

4.2.5. Verification of the Daily Energy Budget of Hamsters

In order to check hamsters' *DEB* thus constructed, the values obtained in the present study were compared with those calculated from the equation

$$DEB \text{ (kcal/g day)} = [2.437 + f\,(2.3278 - 0.1164\,t_a)]\,W^{-0.5} \qquad (12)$$

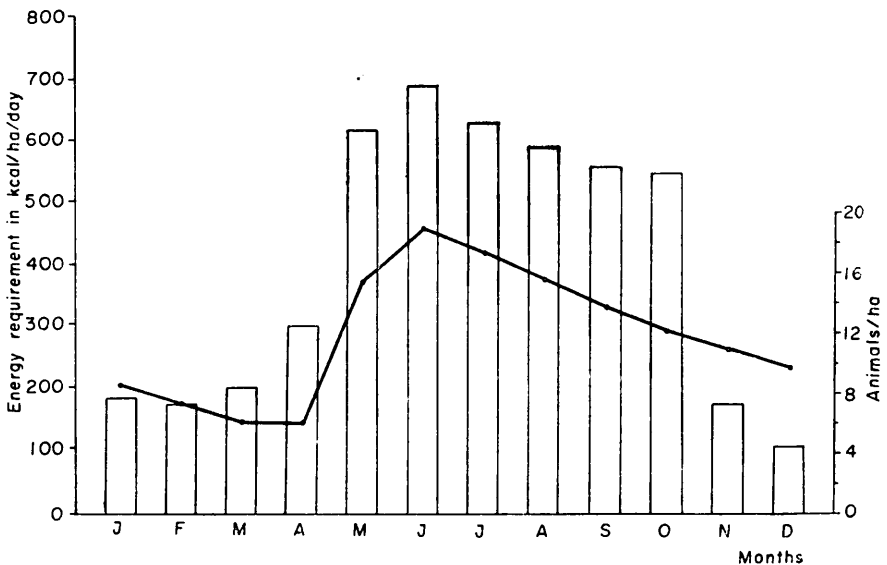suggested by G r o d z i ń s k i & W u n d e r (1975) for rodents and

Fig. 11. Cost of maintenance of hamsters (respiration) over a year. Blocks — dissipation of energy in successive months, solid line — density of hamster population.

based on abundant comparative materials. They compared the budget calculated for *Perognathus* on the basis of the above formula with the results that C h e w & C h e w (1970) obtained using $D_2{}^{18}O$. This comparison, made for two months, showed quite a surprising agreement, which indicates a great accuracy of formula (12).

The *DEB* of the hamster was computed using this very equation for

three summer months, July, August and September. The dissipation of energy averages 0.154 kcal/g day or 44.2 kcal/day for an average animal of the population. An analogous *DEB* calculated in the present study amounts to 0.133 kcal/g day or 38.3 kcal/animal day. Thus the relative error of the budgets computed from G r o d z i ń s k i & F r e n c h's (1974) equation is scarcely 15.4%. This difference is small, for it should be borne in mind that all interspecific equation are, in their very principle, averaged values.

There is also a group of budgets constructed on the basis of *RMR* (T r o j a n, 1969; C h e w & C h e w, 1969; G r o d z i ń s k i & W u n- d e r, 1975). The *DEB* of hamsters was calculated for July from the equation given by C h e w & C h e w (1970). Such a budget consists of two parts: $E_m = E_r + E_a$, where E_m represents the total costs of main- tenance, E_r the metabolic rate at rest and E_a the metabolic rate during activity.

In order to eliminate the costs of activity, which are rather complicated and charged with a grevious error, the values deviating somewhat from the »classical« *RMR* (G e s s a m a n, 1973) were applied here. The basis was here, on the one hand, the minimum metabolic rate of hamsters equal to 0.69 cc/g hr and obtained experimentally on resting animals and, on the other hand, the maximum metabolic rate, 2.11 times as high as the previous one (Section 3.9). This last metabolic rate was assumed both for the hours of activity out of the nest and instead of the addition to the metabolic rate for activity. As the ambient tempera- ture in the study area was above 17°C in July, it was not needed to add any correction for thermoregulation outside the nest to the mean meta- bolic rate established at 15 and 20°C.

DEB thus calculated figures out at 38.1 kcal/animal day and so it resembles that computed for the same month in the present work (36.6 kcal/animal day). Unfortunately, the calculation of such a budget for winter months is very complicated in hibernators, because it must be made up of very many components. Both comparisons quoted seem however to indicate a fairly great veracity of the energy budget of hamsters calculated in this study. An ideal method for verifying such a budget would certainly be the application of marked water or other isotopic techniques, or simultaneous telemetric measurements of tempe- rature, cardiac rhythm and respiratory rhythm directly under field conditions (G e s s a m a n, 1973). This is however very complicated, involves huge expenses and methodical difficulties — deep burrows would much complicated these measurements or made them simply impossible.

4.3. Production and Respiration of Hamster Population

Homoiothermic animals spend a huge majority of assimilated energy

to cover the costs of maintenance (respiration). M c N e i l & L a w t o n
(1970) collected data concerning production and respiration and their
mutual relationship for 12 populations of homoiothermic animals. The
efficiency of production of all the populations compared by these authors
(*P/A*) lies within fairly narrow limits of 1.1—2.9⁰/₀. The mean efficiency
from all these populations is about 1.7⁰/₀. G l i w i c z (1973) calculated
the value of production efficiency for a population of *Proechimys* in an
analogous way and obtained as much as 4.73⁰/₀.

The respiration, production and assimilation of the hamster population
under study are illustrated in Table 9. The values given were used to
calculate the efficiency of production; it is very high in the hamster
population and, coming to 7.2⁰/₀, markedly exceeds the results obtained
by other authors (Table 9). G r o d z i ń s k i & F r e n c h (1974) express
the relationship between production and respiration by means of an
equation based on a rich material of 24 non-hibernating rodent species.

<div align="center">Table 9</div>

<div align="center">Parameters of energy balance of hamster population.</div>

Respiration, R	1.198×10^5 kcal/ha 7 months (activity period)$+2.46 \times 10^4$ kcal/ha
	5 months (hibernation period)$=1.445 \times 10^5$ kcal/ha year
Production, P	$P_r = 1034$ g/ha year; $P_g = 5435$ g/ha year; $\Sigma p = 6469$ g/ha
	$\times$ year $= 1.12 \times 10^4$ kcal/ha year [1]
Assimilation, A	1.557×10^5 kcal/ha year
Consumption, C	2.22×10^5 kcal/ha year
Efficiency of production, ⁰/₀	$P/A = 7.20$; $P/C = 5.04$
P/R, ⁰/₀	7.75

[1] Calorific value (1.74 kcal/g) from F l e h a r t y & C h o a t e, 1973.

If the value of respiration obtained in the present study is substituted
in this equation, the value of production thus received is lowered by
as much as 50⁰/₀. M c N e i l & L a w t o n (1970) give an analogous
formula describing the relationship between production and respiration.
If, in turn, the respiration of hamsters is substituted in it, the actual
production determined in the present work appears to be about 4 times
as high. As previously, the calorific values of body tissues of *Sigmodon*
were used here to convert the biomass into energetic values (F l e -
h a r t y & C h o a t e, 1973).

G r o d z i ń s k i & F r e n c h (1974) also compute production effi-
ciency as *P/R*; obtained in this way for the hamster population, it is
very high (7.8⁰/₀) and exceeds even the maximum values given by these
authors for *Apodemus* and *Sigmodon* (respectively, 6.1 and 6.0⁰/₀). The
fact that the efficiency in the hamster population calculated by the
foregoing methods is evidently higher than in populations of non-

hibernating animals seems quite natural, for the period of hibernation of hamsters permits an enormous reduction in the costs of maintenance under particularly unfavourable environmental conditions.

4.4. Energetics of Continuously and Seasonally Active Animals

If we compare the costs of maintenance calculated from energy budgets for very various groups of animals, much differing in size but active throughout the year, the dissipation of energy appears to be independent of season.

G ę b c z y ń s k i (1965) found that the respiration of the common shrew (*Sorex araneus*) in winter exceeds that in summer of the average by about 24%. R a n d o l p h (1973), who studied the energetics of *Blarina* populations, obtained similar figures. The mean values obtained by him for two populations differing in size were higher by about 30% in winter. G ó r e c k i (1968, 1969) found that in *Clethrionomys glareolus* and *Apodemus agrarius* the summer budgets were higher on the average only by 9.9% than the winter ones.

H a n s s o n & G r o d z i ń s k i (1970) demonstrated that in *Microtus agrestis* the dissipation of energy in summer is 13.8% higher than in winter and 10.6% higher than in autumn, these value being at that established for an average vole in the population in the given season. F l e- h a r t y & C h o a t e (1973), who studied the bioenergetics of a population of relatively large *Sigmodon hispidus*, wrote that the energetic cost of maintenance of this animal in winter is higher only by about 23%.

Lastly, W e i n e r (1975) computed that the respiration of a 22-kilo roedoe in summer is only 20% higher and that of a 25-kilo roebuck 17% higher than in winter. Analogous differences in consumption are about 30% for the female and only 12% for the male.

Then, as can be seen from all these examples, the dissipation of energy in most of the examined populations of animals that are continuously active all the year round is very similar. The greatest differences between winter and summer do not, as a rule, exceed 30%, and in most species are considerably smaller, in spite of drastic changes in weather and food conditions.

On the other hand, the energy expenses connected with the costs of maintenance in seasonally active animals differ diametrically. Unfortunately, as has been mentioned at the beginning, we have at our disposal only very few data.

Tremendous differences in energy requirement over a year were found in three species of the *Gliridae* (G ę b c z y ń s k i *et al.* 1972). The fat dormouse (*Glis glis*) used 88.7—91.8% of the yearly energy requirement in the 6-month period of activity. *Muscardinus avellanarius* dissipated

about 92% of the energy in the same period, not unlike *Dryomys nie-dula*, which utilized as much as 92.5% of its yearly energy budget.

The analogous values obtained for the hamster population indicate that in the winter, while hibernating, these rodents dissipate (respiration) only about 17% of the energy, the rest being spent during their active life.

The calculations for the *Gliridae*, like those in the present study, concern the whole period of hibernation without allowing for short periods in which the animals were awake. These periods having been allowed for, the energy dissipated during true hibernation was naturally still much lower. K a y s e r (1965) observed that in *Spermophilus* the dissipation of energy in 171 days of hibernation was 70 kcal, but in the periods of awakenings, 14 days altogether, the animal spent as much as 580 kcal.

Like hamsters, the *Gliridae* consume their food supplies gathered in the autumn during the breaks in hibernation (G o l l e y, R y s z k o w s k i & S o k u r, 1975). The lower dissipation of energy than in hamsters can be explained in the *Gliridae* by a greater amount of energy deposited in the form of adipose tissue, *e.g.* in the grey squirrel fat constituted as much as 40% of body tissues before hibernation (G ę b c z y ń s k i *et al.*, 1972). Such deposition of adipose tissue, rather expensive in energy (K i n g & F a r n e r, 1961; B l a x t e r, 1966), in turn, causes also an increase in the total energy expenses in the period of activity.

Finally, there is another essential difference between the groups of animals under discussion, namely, the pressure exerted on the ecosystem varies with season in a different way. The continuosly active animals, as a rule, exercise the greatest influence on the ecosystems in the pre-vernal season and early spring. The destruction of even a small number of plants in the spring may have a tremendous effect on the final yield (J u d e n k o, 1967; T e r t i l, 1974). On the other hand, hibernators exert the strongest pressure on the agrocenoses in the late summer and autumn.

To sum up, hibernators have a completely different influence upon the ecosystem from that of continuously active animals, in which the daily energy budgets show relatively small fluctuations in different seasons of the year. In summer both groups of animals act in a similar way in the chains of energy flow, whereas in winter hibernators are completely excluded from these chains.

4.5. Effect of Hamster Population upon Crops

The production of crops which are potential food for hamsters was calculated on the basis of their average structure in the fields examined and the data concerning the efficiency of different crops (N i e w i a d o m-

s k i, 1971; P a w l i c k i, 1974). Such an »average« hectare offers both substantial foodstuffs (seeds of cereal plants, *Vicia faba*, maize and sunflower) and green forage (wheat, rye, maize, lucerne, grass and sunflower) to these animals during the year. The yearly yield of green forage averages 56.7 q. of dry matter/ha or about 2.27×10^7 kcal/ha and that of grain 31.2 q. or about 1.40×10^7 kcal/ha. There is 3.67×10^7 kcal of food altogether in 1 hectare in a year (vegetative season).

If we assume that the coefficient of assimilation is 70% (mean value from own data and those given by E r d a k o v, 1972) (Table 9), the whole population of hamsters consumes 1.84×10^5 kcal/ha during the 7-month period of active life. This result must however be augmented by the value of foodstuffs uneaten but spoilt, which may be very various and even exceed the consumption by many times (T e r t i l, 1974; Z l o- t i n, 1975). If hamsters destroy as much food as they eat up, the effect, approximately only 1%, is still relatively small. Z l o t i n (1975) however found that in grass land ecosystems the consumption constitutes scarcely 5% of the total impact of rodents, whereas the whole rest consists just of these destroyed foods and other effects of these animals resulting in a lowering of the yield.

The impact of hamsters was found to be tremendous in autumn, when in addition to foraging these animals begin to store food. Their provisions consist chiefly of grain (K a r a s e v a & S h i l a y e v a, 1965; P e t z s c h, 1965; W a l k e r, 1964) and thus they influence the yield directly at that time. If we assume that each hamsters stores about 15 kg of food and that at that time (August—October) the mean number of hamsters approaches 14 individuals/ha (Table 8), they all together gather above 200 kg of food. The mean calorific value of these supplies is about 4 kcal/g, because, as has been mentioned, they consist chiefly of grain, the water content of which is very low. Thus the supplies gathered by hamsters in an area of 1 ha amount to as much as 8.32×10^5 kcal. As the output of grain is about 1.4×10^7 kcal/ha yr, the impact of hamsters on the crops in this period is very considerable; it reaches a considerable figure of 5.9% in their food caches only.

If we increase this figure by adding the estimate of consumption and correcting it using the above-mentioned indices (Z l o t i n, 1975) of the consumption: dectruction ration, the immense impact of hamsters on the grops becomes evident.

As can be seen from the foregoing calculation, hamsters can »compete« fairly successfully with man in harvesting the ultimate crop.

The impact of rodents on different ecosystems does not, as a rule, exceed 2% (C h e w & C h e w, 1970; G e s s a m a n, 1974; G o l l e y, R y s z k o w s k i & S o k u r, 1975). A 20% decrease in crops was observ-

ed only in the case of *Microtus arvalis* (R y s z k o w s k i, G o s z c z y ń-
s k i & T r u s z k o w s k i, 1973). This situation was however exceptional,
taking place during a heavy outbreak of these rodents. Among the ma-
terials presented by G o l l e y *et al.* (1975) there is, in addition, a case of
the $12^0/0$ impact of *Peromyscus*, but this impact has been determined only
in relation to grass seeds, the production of which is relatively low.

Even if we use the values concerning the primary production accessible
to animals (C h e w & C h e w, 1970), most ecosystems are utilized by ro-
dents, as a rule, in $1.6—5.8^0/0$.

Againts a backround of these results the findings obtained by A b a t u-
r o v, R a k o v a & S e r e d n e v a (1975) are particularly relevant. They
concern the impact of sousliks, which, like hamsters, are only seasonally
active, on grassland ecosystems. The pressure of these animals was ex-
tremely high, ranging from 10 up to $38^0/0$ in different years. These
values by many times exceed both the values calculated in the present
study and those listed by C h e w & C h e w (1970) and G o l l e y *et al.*
(1975) for different rodent populations. This was connected, on the one
hand, with a very great abundance of sousliks (36—66 individuals/ha)
and, on the other hand, with the low productivity of these ecosystems
and their great accessibility to these animals. Neither of these facts
however explains completely such a tremendous impact of sousliks on
the ecosystem. Being seasonally active animals, sousliks seem to have
to secure food supplies for the rest of the year, apart from their normal
consumption, in a relatively short time, which, naturally, brings about
this great overestimation of their total impact of the ecosystem, examin-
ed only during the period of active life.

In considering the impact of hamsters on agrocenoses, one must not
omit their beneficial influences. The first of them results from their
subterraneous mode of life. While digging their tunnels, hamsters dislodge
huge amounts of soil and from a very great depth at that. G o l l e y *et al.*
(1975) present a comparison of the amounts of soil removed by different
animals, but it does not include the hamster. The knowledge of burrows
of hamsters (K a r a s e v a & S h i l a y e v a, 1965) permits the calcula-
tion which shows that, digging its burrows, a hamster must transport
about 1 m^3 of soil yearly, often from a depth approaching 2 m. Such
dislodgments of soil are of enormous importance to the distribution of
chemical compounds. A b a t u r o v & Z u b k o v a (1969) write that
1500 kg of soil/ha yr removed by *Citellus* in the steppe contained 5 kg
of Na, 77 kg of Ca, 122 kg of Al, 18 kg of S, and many other equally
important biogens.

Another problem is the fertilization of soil by hamster populations.
An average 400-gram hamster, which takes only 10.5 g of dry matter in

food daily, returns 2.5 g of faeces and urine to the ecosystem. The yearly energy budget of these rodents indicates that at a mean assimilation coefficient the consumption is 2.2×10^5 kcal/ha (Table 9). Thus, about 15 kg of faeces and urine must be returned to each hectare of cultivated fields during a year. Here we must add huge food stores, which are probably never used up (Section 4.2.3.). If only 25% of the food cache remains unused, which the amount of organic matter which returns to the ecosystem increases by about 30 kg/ha yr. This amount is small in comparison with the data given by K u c h e r u k (1963) for steppe rodents of Eurasia, which produced up to 250 kg of excreta/ha. It is however very rich in nitrogen (D r o ż d ż, 1968) and accelerates the circulation of matter very much; it may also have an effect on the increase in vegetable production. U l e h l a, P e l i k a n & Z i c h o v a (1974) found that lucerne around the burrows of hamsters, especially old ones, was much higher and had its biomass markedly larger, which was naturally due to the particularly intense »fertilization« of the field in in the vicinity of these burrows.

The harmful impact of hamsters on crops may also be compensated to a small degree by the destruction of invertebrates noxious to agriculture, but vegetable foodstuffs prevail decidedly in the diet of these rodents (G ó r e c k i & G r y g i e l s k a, 1975).

The range of hamsters in Poland is fairly wide, for they occur in the whole south-eastern part of the country up to the line connecting the towns Zielona Góra, Poznań, Płock and Białystok (S u r d a c k i, 1963, 1971, 1973). In spite of their discontinuous distribution, the impact of hamsters on agrocenoses seems to be very great by standards of the whole country.

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Andrzej GÓRECKI

PRZEPŁYW ENERGII PRZEZ POPULACJĘ CHOMIKÓW

Streszczenie

Badania nad przepływem energii przez populację chomików *Cricetus criceus* (L i n n a e u s, 1758) oraz ich wpływem na uprawy prowadzono na 128 ha pól leżących w dolinie Wisły — 80 km od Krakowa (Ryc. 1). Liczebność dorosłych chomików określano wiosną i jesienią każdego roku przez liczenie czynnych nor (Tabela 1). Średnie roczne zagęszczenie dorosłych zwierząt wynosiło 8,5/ha. Po uwzględnieniu młodych zwierząt, których ilość oszacowano z liczby embrionów całkowite zagęszczenie wynosi rocznie średnio 12,4 chomików/ha (Ryc. 2). Na podstawie zależności ciężarów ciała i ciężarów soczewek oka chomików ustalono strukturę wiekową tych gryzoni (Ryc. 3, Tabele 2, 3, 4). Z kolei pozwoliło to na ułożenie tabel życia populacji chomików (Tabela 5, Ryc. 4).

Produkcja populacji chomików wynosi w ciągu roku 6,5 kg/ha, z czego na produkcję rozrodu przypada tylko 1,03 kg/ha. Rotacja biomasy całej populacji jest równa 1,40, a średnia długość życia wynosi około 7 miesięcy.

Rytm aktywności dobowej chomików był zarówno latem, jak i jesienią dwuszczytowy. Latem aktywność poza norą trwała około 3,5 godziny, a jesienią ponad 6 godzin na dobę (Ryc. 6). Głębokie temperatury ciała, mierzone telemetrycznie u chomików eksponowanych w 15 i 20°C nie różniły się między sobą i całą dobę oscylowały pomiędzy 37 i 38°C (Ryc. 10). Średni metabolizm dobowy chomików w 15°C wynosił 1,00, a w 20°C 1,08 cm^3 O$_2$/g godz, przy czym metabolizm maksymalny (1,45 cm^3 O$_2$/g godz) przewyższał minimalny 2,11 razy (Tabela 6, Ryc. 8, 9). Zależność metabolizmu (M — cm^3 O$_2$/g godz) i ciężaru ciała (W) miała postać:

$$M = 162,9 \, W^{-0,883} \quad \text{(Ryc. 7)}$$

Oceniono dobowe budżety energetyczne populacji chomików w cyklu rocznym (Tabele 7, 8). Taki budżet (respiracja) waha się od 105,9 w grudniu do 704,9 kcal/ha/dzień w czerwcu (Ryc. 11). Asymilacja populacji wynosi 1.56×10^5 kcal/ha/rok, a stosunek produkcji do niej wynosił 7,2% (Tabela 9).

W oparciu o średnią strukturę zasiewów i wydajność produkcji oraz o liczebność chomików i ich konsumpcję, udało się oszacować wpływ tych gryzoni na ekosystemy. Latem ich wpływ powodowany konsumpcją jest niewielki i nie przekracza 1%. Natomiast jesienią, gdy chomiki gromadzą przysłowiowe zapasy pokarmowe, ich wpływ wzrasta do około 6% nie wliczając w to pokarmów zniszczonych.