EKOLOGIA POLSKA (Ekol. pol.)	22	3/4	617–634	1974

Alicja BREYMEYER

Department of Biocenology, Institute of Ecology,
Polish Academy of Sciences, Dziekanów Leśny near Warsaw

ANALYSIS OF A SHEEP PASTURE ECOSYSTEM IN THE PIENINY MOUNTAINS (THE CARPATHIANS)

XI. THE ROLE OF COPROPHAGOUS BEETLES (*COLEOPTERA, SCARABAEIDAE*) IN THE UTILIZATION OF SHEEP DUNG*

ABSTRACT: Analysis was made of variations in density, biomass and species structure of coprophagous beetles over the course of two seasons (May-September in 1970 and 1971). A total of 16 species of beetles of the *Scarabaeidae* family were found both in sheep excrement and in the 10-centimetre layer of soil beneath the excrement. The imagines of *Scarabaeidae* make their appearance in one-day old excrement (after 1 day's exposure of sheep dung on the pasture), and the larval forms slightly later. It was calculated that during a season the imagines of scarabs carry from 12–33 g d.wt. of sheep excrement per 1 m^2 of pasture into the soil.

Contents

---

*Praca wykonana w ramach problemu węzłowego nr 09.1.7 (grupa tematyczna „Produktywność ekosystemów trawiastych").

1. INTRODUCTION

In the ecosystem of mountain pastures grazed by sheep one of the main trophic links is undoubtedly the chain of coprophagous species. Sheep droppings are organic matter only slightly transformed but well prepared for further utilization (crumbled, moist, with developed microflora). Coprophagous invertebrates carry out this utilization.

It is known from the biology of scarabs that the coprophilous species of this family feed on the excrement of mammals, live in it and also lay eggs in it (Reitter 1909, Schmidt 1935, Balthasar 1964, Bornemissza 1969). Some species carry fragments of excrement to the soil and it is there, in the holes dug for the purpose, that the eggs are laid. The largest scarabs of our climatic zone – *Geotrupes* Latr. sp. and *Copris* Gffr. sp. – build a whole system of tunnels and holes, roll large balls of sheep excrement and lay eggs in them. After hatching, the larvae feed on the excrement and remain in it until they pupate. The imago of the insect emerges from the soil. In Polish grassland habitats the two above-mentioned genera of largest coprophages are rarely encountered, while species of the genera *Aphodius* Ill. and *Ontophagus* Latr., which utilize the excrement lying on the pasture and the shallow layer of soil below it, are very frequently found. They belong to the most numerous and most important coprophages on pastures in our climatic zone (Schmidt 1935, Goljan 1953, Olechowicz 1974).

The purpose of this study is to present the composition, variations in numbers and biomass of populations of scarabs on a mountain pasture at Jaworki. Using data given by other authors, and also unpublished materials, an attempt has been made at assessing the amount of sheep excrement transported by scarabs into the soil.

2. MATERIAL AND METHODS

The material was collected on a mountain pasture at Jaworki during the period from May-September in 1970 and 1971 (a detailed description of working stations is to be found in the following studies: Czerwiński, Kotowska and Tatur (1974), Traczyk and Kochev (1974), Czerwiński and Tatur (1974). The study pastures are situated at approx. 700 m above sea level; they consist partly of cultivated fields abandoned about 30 years ago. Sheep graze there from the beginning of May to the end of September each year. It is difficult to estimate the actual density of sheep in the study area of the pasture: the flocks are constantly driven to different areas of the pasture, so that parts of the area are grazed with a different degree of intensity on different days. Our working station, known as Owcza Droga (Sheep Way), was situated on the path of the flock leading to the more distant parts of the pasture. The sheep were driven along there 2–4 times daily (in the morning, during their return for the noon milking, then again in the afternoon when the sheep go out again on to the pasture, and when they return in the evening). The number of sheep was not estimated in the studies on coprophagous species, only the density of excrement on the pasture. The amount of excrement was counted every month on 10 areas 1×10 m chosen at random (cf. Olechowicz 1974).

The scarabs were captured in excrement and in the soil beneath them (layer about 10 cm deep). A detailed description of the method used is to be found in the study by Olechowicz (1974); it will only be mentioned here that the scarabs were collected in so-called monthly "cycles". The freshly collected sheep droppings were weighed and spread out on the pasture, then, at first daily and later every few or every several days, 10 droppings were taken from the pasture and all the insects present in them collected. Frequency of sampling was as follows: in 1970 – every month, on the 1st, 2nd, 3rd, 4th, 5th, 10th and 30th day from the time of spreading excrement on the pasture; in 1971 – every month on the 1st, 3rd, 6th, 10th, 15th and 30th day from the time the excrement was spread on the pasture. Insects were always additionally collected from the soil beneath the excrement, taking a cylindrical soil sample about 10 cm in depth and 10 cm in diameter for this purpose. The soil was sorted by hand on the spot or in the

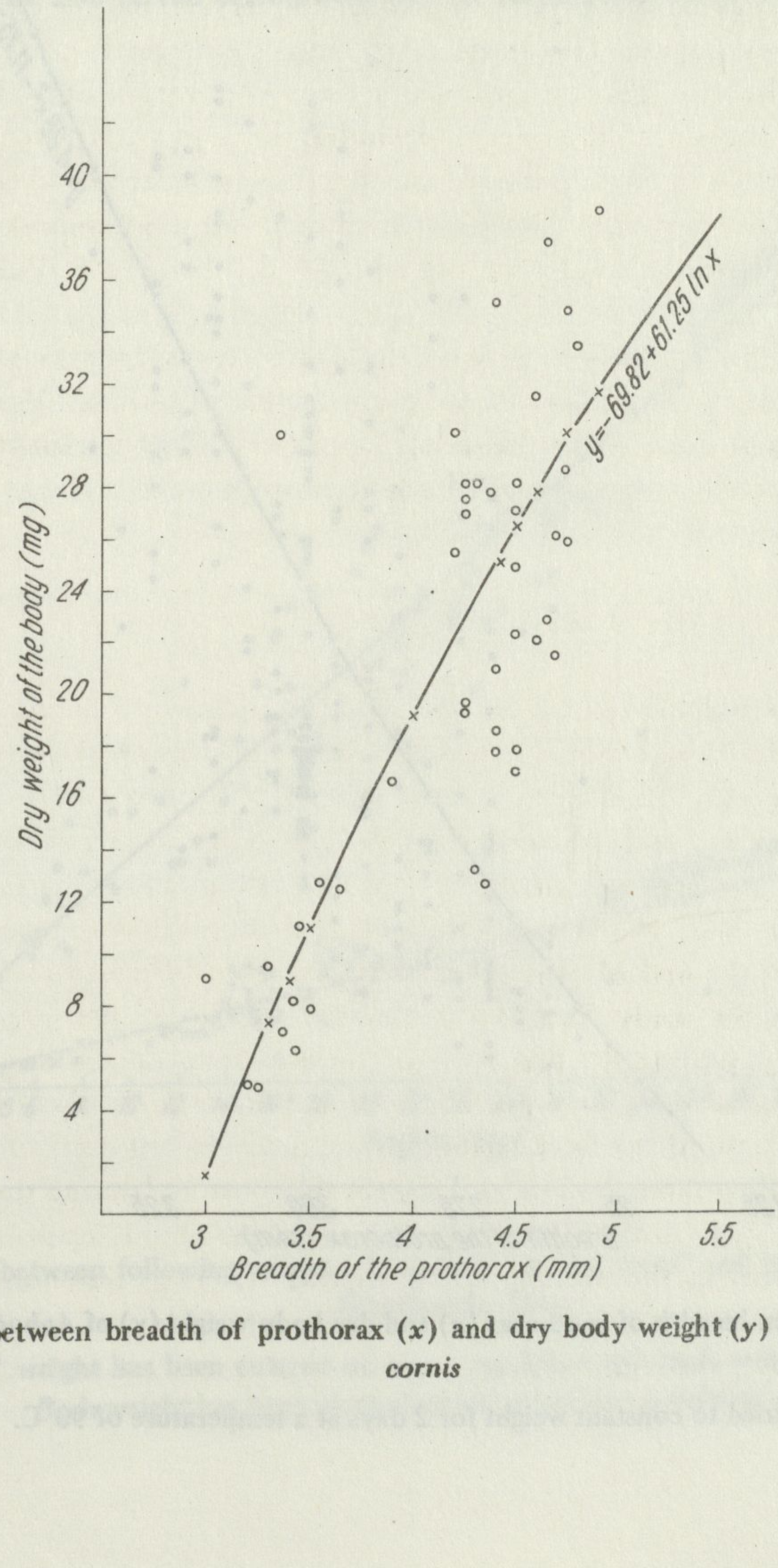

Fig. 1. Relation between breadth of prothorax (x) and dry body weight (y) of *Ontophagus fracticornis*

laboratory. Only the coprophagous beetles of the *Scarabaeidae* will be dealt with here – the other groups of coprophilous invertebrates ("coprobionts") have been elaborated by O l e c h o w i c z (1974).

The body mass of the scarabs was estimated as follows:

(1) Measurements of the prothorax of imagines was done by means of a nonius. It had previously been found, from several hundred measurements of scarabs, that the coefficient of correlation between breadth of prothorax and dry weight[1] of the insect is high,

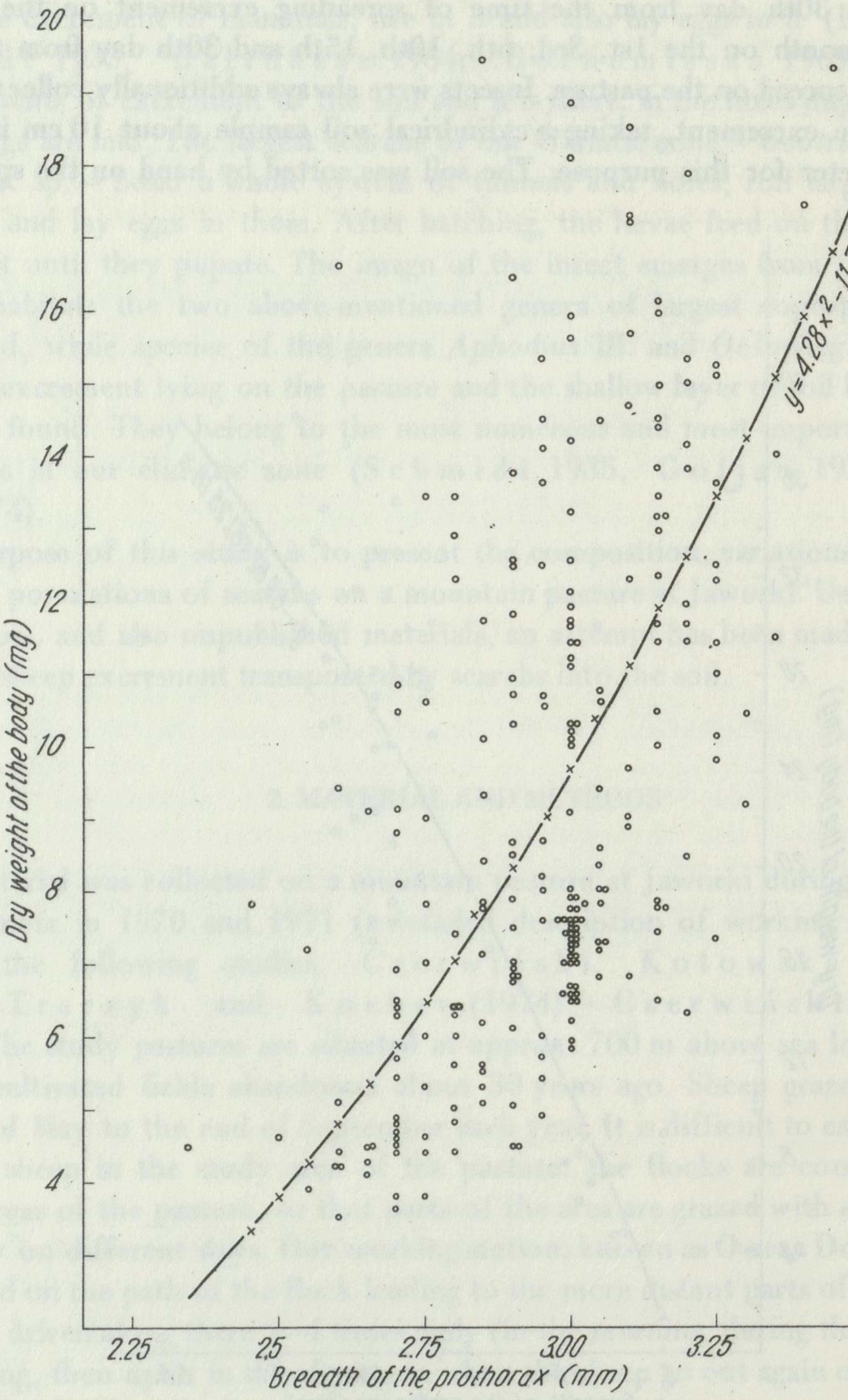

Fig. 2. Relation between breadth of prothorax (x) and dry body weight (y) of *Aphodius fimetarius*

[1] The insects were dried to constant weight for 2 days at a temperature of 90°C.

varying from 0.68–0.71. Calculation was next made of the relation between breadth of prothorax and dry weight of body for the two species dominating in the area: *Aphodius fimetarius* L. and *Ontophagus fracticornis* (Preyssl.). Curves showing the character of these relations and the equations describing them are given in Figures 1 and 2. The whole material collected and conserved in alcohol was measured with a nonius and its dry mass calculated by means of the above equations. It was accepted here that all species of the genus *Ontophagus* have a similarly shaped body and the equation found for *O. fracticornis* was applied to them. For species of the genus *Aphodius* we used the equation found for *A. fimetarius*, calculation of which was based on a very large number of measurements of individuals differing in size. It was assumed that all species of the genus *Aphodius* have a similarly shaped body and therefore the same relation between breadth of the prothorax and dry weight.

(2) A total of 200 larvae of *Scarabaeidae* of varying size from 0.45 mg fresh weight to

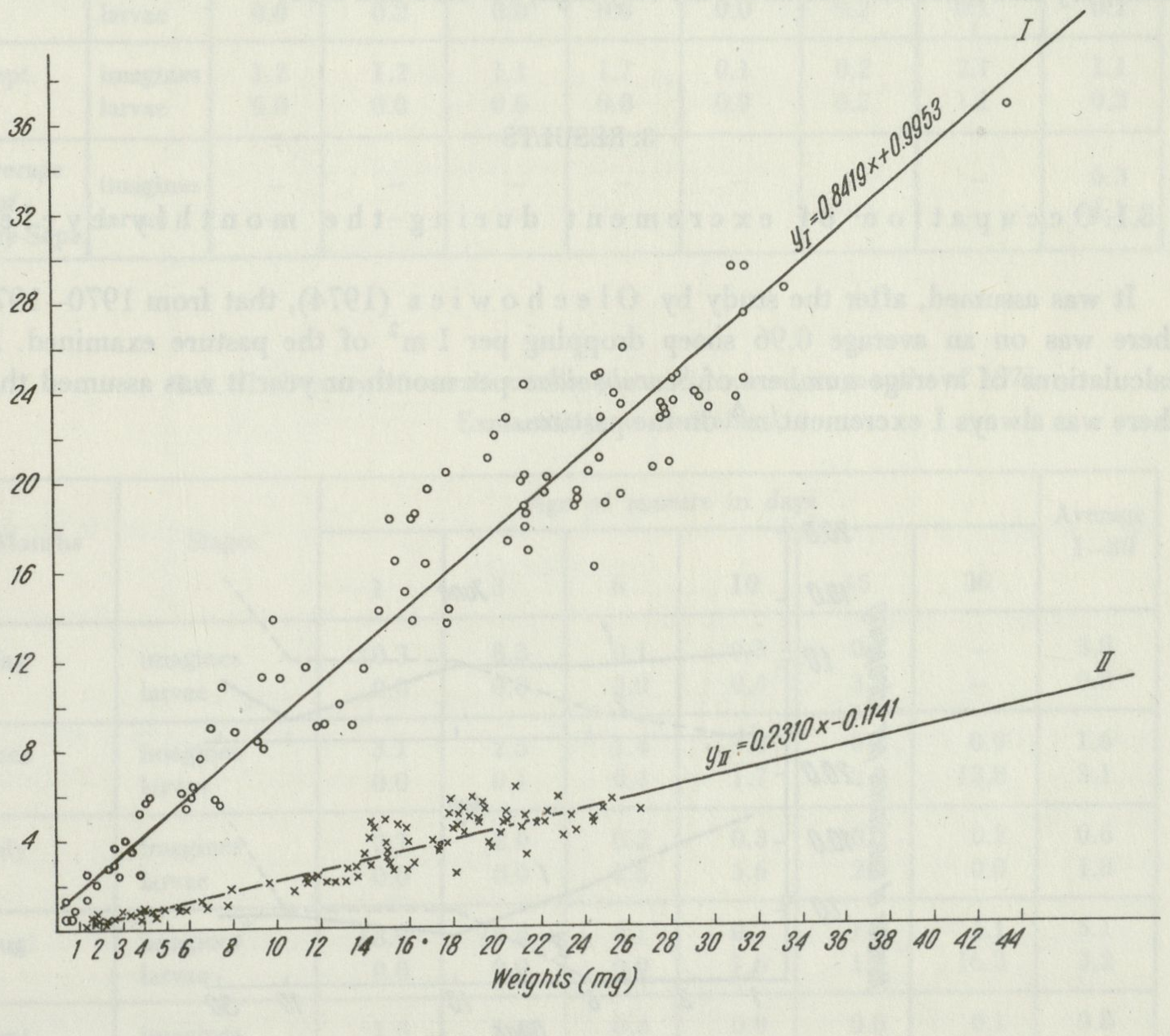

Fig. 3. Relation between following weights: fresh and "alcohol fresh" and between fresh and dry for *Scarabaeidae* larvae

"Alcohol fresh" weight has been entered on axis x for line I and fresh weight on axis y. For line II fresh weight has been plotted on axis x and dry weight on axis y

36.2 mg f.wt. were collected. All the larvae were weighed with accuracy to 0.01 mg, and the collection was next divided into halves: 100 larvae were dried at a temperature of 90°C to constant weight, weighed again and calculation made of the correlation between fresh and dry weight. Line *II* on Figure 3 represents this relation; on an average scarab larvae lose 77% of weight during drying. The second half, also weighed in this way, was conserved in 70% alcohol. After 8 weeks the larvae were removed, dried on filter paper and weighed – this giving the so-called "alcohol-fresh" weight. The correlation was calculated between fresh and alcohol fresh weight (Fig. 3, line *I*); using this correlation it is possible to estimate fresh weight of the animals on the basis of collections kept in alcohol. The following procedure was adopted for the whole of the material collected and preserved in alcohol; all preserved individuals were weighed, fresh weight was calculated for them on the basis of equation y_I, and then dry weight calculated on the basis of equation y_{II} (Fig. 3).

Correlation coefficients calculated for the relation between the following weights: fresh, dry and „alcohol" for larvae are very high, i.e. 0.96 and 0.98.

3. RESULTS

3.1. Occupation of excrement during the monthly cycle

It was assumed, after the study by Olechowicz (1974), that from 1970–1971 there was on an average 0.96 sheep dropping per 1 m² of the pasture examined. In calculations of average numbers of *Scarabaeidae* per month or year it was assumed that there was always 1 excrement/m² on the pasture.

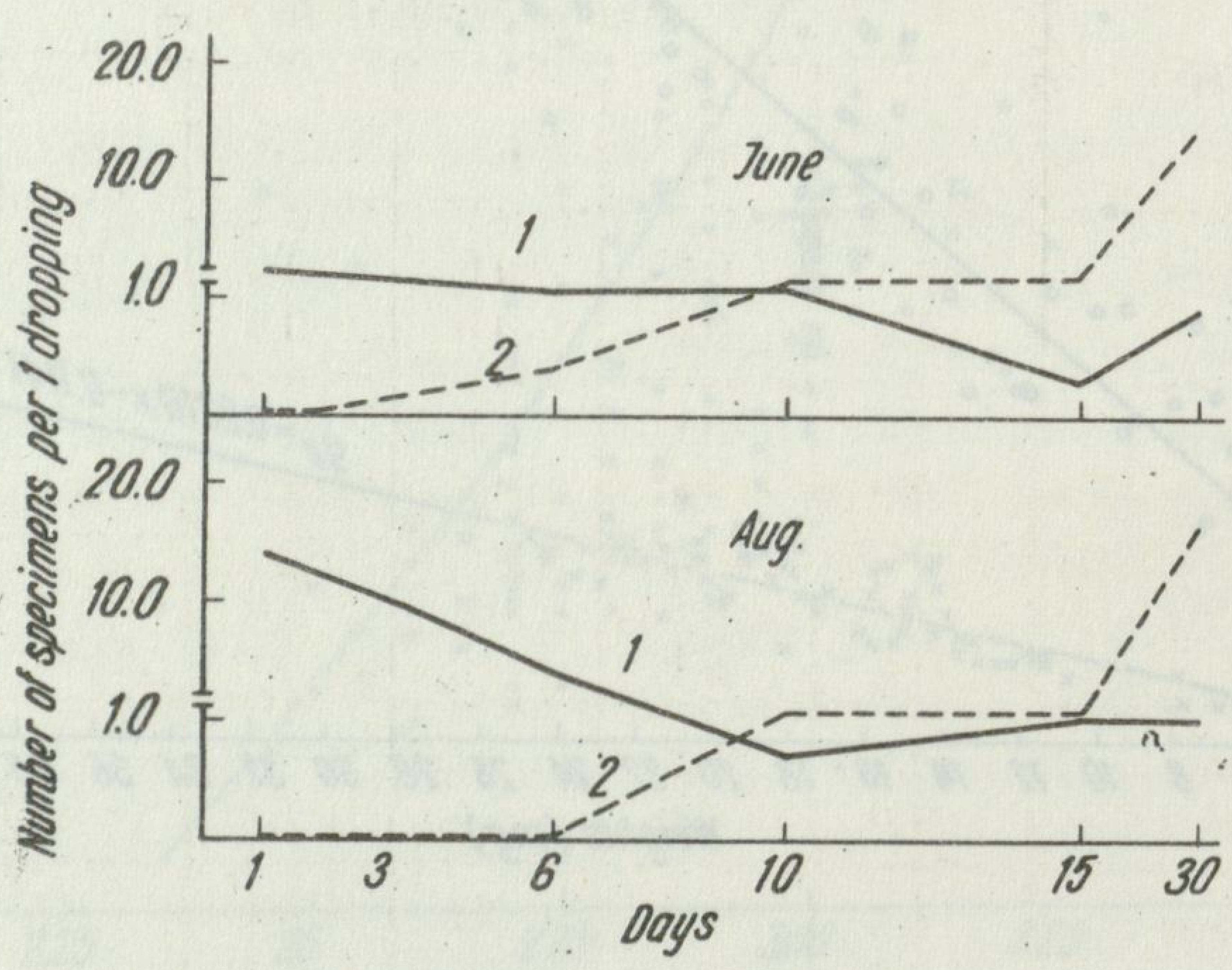

Fig. 4. Numbers of *Scarabaeidae* on successive days of the „ageing cycle of the dung" in two months in 1971. Mean values from 10 samples containing dung and 10 cm soil layer

1 – imagines, *2* – larvae

Tab. I. Density of scarabs on the pasture in successive months of 1970. Each figure is the average of 10 samples and represents the number of individuals per 1 dropping and the 10 cm layer of soil beneath the dung

Months	Stages	Age of manure in days							Average
		1	2	3	4	5	10	30	1–30
May	imagines	40.3	–	14.2	–	–	–	0.0	18.2
	larvae	0.0	–	0.0	–	–	–	3.0	1.0
June	imagines	8.2	25.6	9.0	4.7	7.9	0.6	3.6	8.5
	larvae	0.2	1.6	0.3	1.9	0.8	13.3	4.2	3.2
July	imagines	9.2	10.0	0.4	0.8	1.1	0.6	0.3	3.2
	larvae	0.0	0.6	0.6	0.4	1.1	0.9	1.8	0.8
Aug.	imagines	1.4	0.8	0.5	0.1	0.3	0.4	0.5	0.7
	larvae	0.0	0.2	0.0	0.0	0.0	0.2	0.1	0.1
Sept.	imagines	1.2	1.2	1.1	1.7	0.1	0.2	2.1	1.1
	larvae	0.0	0.0	0.0	0.0	0.0	0.3	1.1	0.2
Average of May-Sept.	imagines	–	–	–	–	–	–	–	6.3
	larvae	–	–	–	–	–	–	–	1.1

Tab. II. Density of scarabs on the pasture in successive months of 1971

Explanations as for Table I

Months	Stages	Age of manure in days						Average
		1	3	6	10	15	30	1–30
May	imagines	10.3	8.3	0.1	0.3	0.1	–	3.8
	larvae	0.0	0.0	0.0	0.4	3.8	–	0.8
June	imagines	3.1	2.5	1.4	1.6	0.3	0.9	1.6
	larvae	0.0	0.1	0.4	1.7	2.3	13.8	3.1
July	imagines	0.7	2.0	0.2	0.3	0.3	0.2	0.6
	larvae	0.0	0.0	2.6	5.6	2.3	0.0	1.8
Aug.	imagines	13.9	10.4	3.7	0.7	1.0	1.1	5.1
	larvae	0.0	0.0	0.0	1.6	1.3	16.3	3.2
Sept.	imagines	1.5	1.5	0.4	0.9	0.6	0.1	0.8
	larvae	0.0	0.0	0.0	0.0	0.0	0.2	0.03
Average of May-Sept.	imagines	–	–	–	–	–	–	2.4
	larvae	–	–	–	–	–	–	1.8

In the two successive study years (1970–1971) *Scarabaeidae* occurred in the following densities on the pasture examined[2] (Tab. I, II): imagines 2.4–6.3/1 dropping, larvae 1.1–1.8/1 dropping. Maximum numbers of imagines (Tab. I) occured in May and June 1970: 26–40 individuals/1 dropping, and in 1971 in May and August: 10–14 individuals/1 dropping. Figure 4 gives an example of the course taken by variations in numbers of *Scarabaeidae* on successive days of the „ageing cycle of excrement". A recurring tendency is occupation of excrement by imagines during the first days of the cycle. On the 6–10th day there is most often a decrease in the number of imagines in excrement, and later either a renewed increase in numbers (June, 1971) or a continued decrease. Larvae (Fig. 4) exhibit an increase in numbers on successive days of „the cycle", which is obvious since they either hatch in the excrement examined from the eggs laid there by imagines, or reach the excrement from the soil.

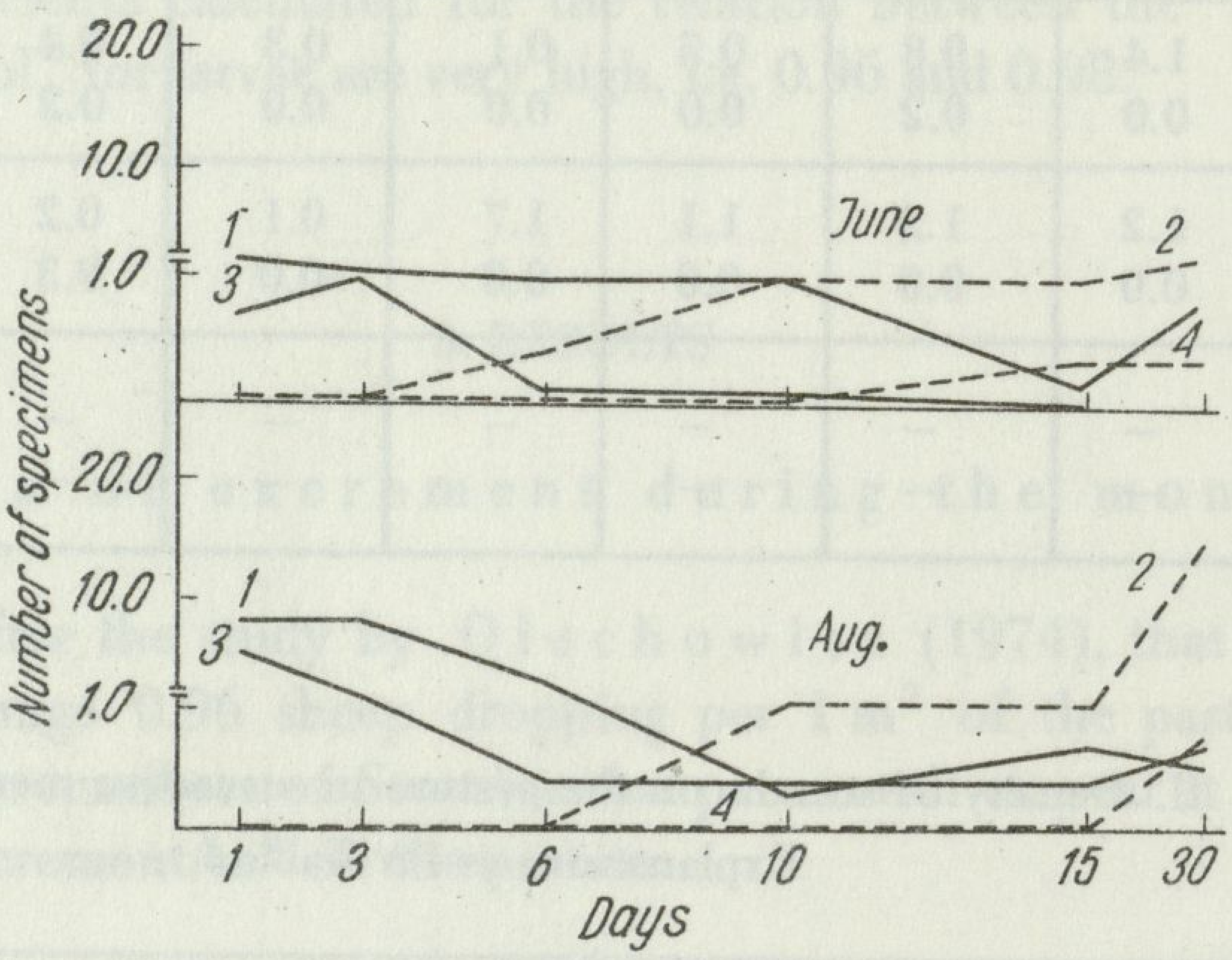

Fig. 5. Numbers of *Scarabaeidae* on successive days of „the ageing cycle of excrement" in the dung and in the soil

Excrement: *1* – imagines, *2* – larvae. Soil: *3* – imagines, *4* – larvae. Mean values from 10 samples

Separate figures have been given of insects occurring in excrement and in the soil under it (data given as examples – Figure 5). The number of both imagines and their larvae are often greater in excrement than in the soil. No sequence of curves in time is found here which could suggest that occupation of excrement takes place first, and then descent of the animals into the soil later. If this moving process does in fact take place it must do so continually and in both directions, i.e. both from excrement-soil and from soil-excrement. This is indicated by the fact that parallel lines illustrating variations in the number of beetles and their larvae in both levels of the habitat examined (excrement and soil) are frequently found. Therefore the more beetles enter the excrement, the more of them move into the soil. Larvae were found to occur periodically in greater numbers in

[2]If only the last days of the cycle are taken into consideration i.e. the 10th and 30th, then we obtain far higher (double) numbers and average biomasses. This is due to the fact that as they hatch out there are increasingly large numbers of larvae in the excrement.

Tab. III. Biomass of scarabs (mg d.wt.) on the pasture in successive months of 1970
Explanations as for Table I

Months	Stages	Age of manure in days							Average 1–30	Average 10–30
		1	2	3	4	5	10	30		
May	imagines	403.30	–	149.93	–	–	–	0.00	184.41	–
	larvae	0.00	–	0.00	–	–	–	8.82	2.94	8.82
June	imagines	70.92	197.68	68.25	37.32	62.98	8.05	57.22	71.77	–
	larvae	0.31	2.51	5.56	1.97	6.57	35.51	20.34	10.38	26.18
July	imagines	102.12	50.82	3.17	3.99	18.46	1.28	2.07	25.98	–
	larvae	0.00	0.86	2.53	0.07	1.45	0.32	3.20	1.20	1.75
Aug.	imagines	12.18	12.11	3.37	1.28	4.64	4.08	6.81	6.35	–
	larvae	0.00	0.04	0.00	0.00	0.00	1.50	9.04	1.51	5.27
Sept.	imagines	10.44	8.52	29.00	26.53	2.57	1.69	21.21	14.28	–
	larvae	–	0.00	0.00	0.00	0.00	0.74	2.99	0.62	1.86
Average of May-Sept.	imagines	–	–	–	–	–	–	–	60.56	–
	larvae	–	–	–	–	–	–	–	3.33	8.77

Tab. IV. Biomass of scarabs (mg d.wt.) on the pasture in successive months of 1971
Explanations as for Table I

Months	Stages	Age of manure in days						Average 1–30	Average 10–30
		1	3	6	10	15	30		
May	imagines	66.19	50.41	1.95	1.61	0.55	–	24.14	–
	larvae	0.00	0.00	0.00	2.37	17.68	–	4.01	10.02
June	imagines	18.66	23.27	12.73	14.72	2.09	6.90	13.06	–
	larvae	0.00	2.86	2.38	2.84	4.81	12.24	4.19	6.63
July	imagines	7.30	20.92	1.83	2.79	3.39	1.30	6.26	–
	larvae	0.00	0.00	1.20	11.14	5.64	0.00	2.99	5.59
Aug.	imagines	227.43	121.11	24.14	16.12	9.44	13.77	68.67	–
	larvae	0.00	C.00	0.00	0.33	25.68	57.98	13.99	27.99
Sept.	imagines	16.68	36.36	0.62	12.86	7.30	2.11	12.66	–
	larvae	0.00	0.00	0.00	0.00	0.00	0.54	0.09	0.18
Average of May-Sept.	imagines	–	–	–	–	–	–	24.96	–
	larvae	–	–	–	–	–	–	5.05	10.08

the soil than in excrement in following four cases (May, June and July 1970, June 1971); rarely larvae were even observed to occur earlier in the soil than in excrement. This can probably be explained by the fact that some of the larvae enter the excrement from the soil. This is, however, a far rarer situation than occupation of excrement by larvae hatching in it and the consequent earlier appearance of larvae in excrement than in soil.

3.2. Numbers and biomass of *Scarabaeidae* during the season

The biomass of imagines and larvae of *Scarabaeidae* are given in Tables III and IV.

On an average there are from 3.33–5.05 mg dry weight of larvae and 24.96–60.56 mg of dry weight of imagines in one sheep dropping. The two developmental stages of *Scarabaeidae* together give a total of 63.7 mg of d.wt./1 dropping in 1970 and 30.1 mg d.wt./1 dropping in 1971. The average weight of one dropping spread out on the pasture for occupation by animals during the "ageing cycle" is, according to Olechowicz (1974) 7.5 g d.wt. During the thirty-day observation period in the "ageing cycle", excrement loses 35% of its original weight. The biomass of *Scarabaeidae* (30–64 mg d.wt./1 dropping) is thus 0.6–1.3% of the mass of the excrement they occupy (counting from the mass of excrement towards the end of the cycle).

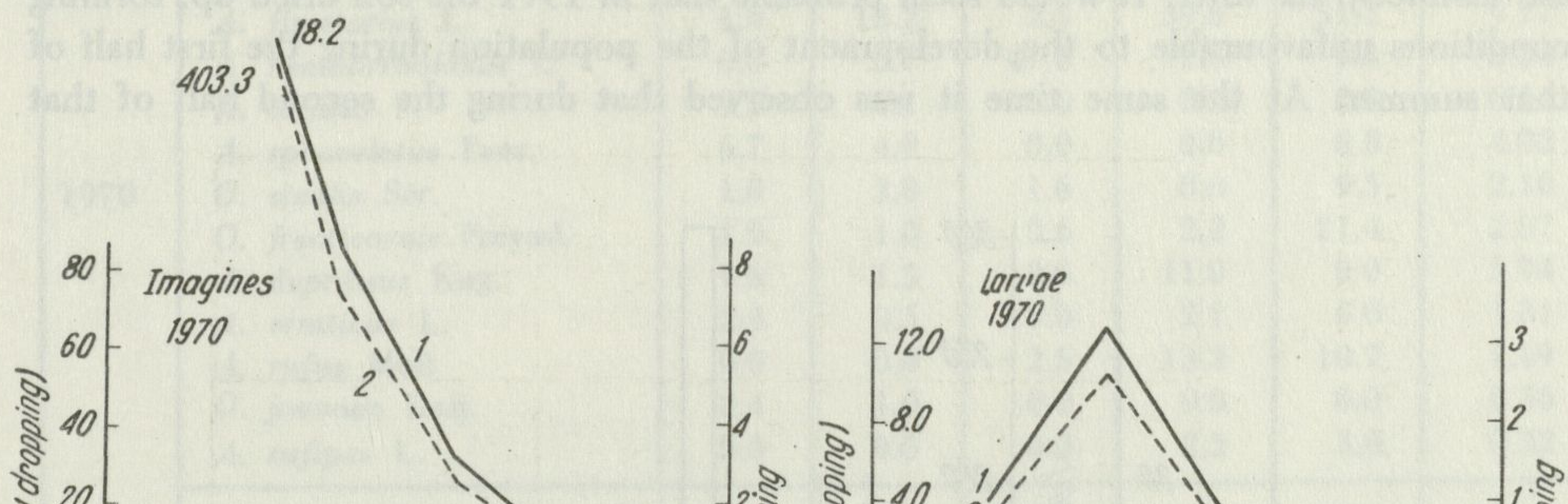

Fig. 6. Numbers and biomasses of *Scarabaeidae* in successive months of the seasons 1970 and 1971

Mean values for all days of the „cycles" and for 10 samples at each point of the „cycle". *1* – numbers of individuals, *2* – biomasses

The course taken by variations in the biomass of imagines is similar to the variations in their numbers (Fig. 6), which is obvious, as the body weight of imagines does not in principle alter. In the two years a slight increase in body weight is, however, observed in the beetle population towards the end of summer (the biomass curve rises above the curve of numbers). Without an appropriate analysis of material it is impossible to say whether this is connected with increase in the body weight only in females laying eggs at that time, or whether this is the autumn increase in body weight of all individuals in the population observed in insects before hibernation. During the first part of the season as regards larvae, the curves of numbers and of biomass are observed to diverge (Fig. 6), which is understandable for two reasons: in the first place, this is a growing population (development of larvae), and in the second new individuals can supplement the populations twice a year. When comparing 1970 and 1971 it is found that during the first half of 1971 the numbers of larvae are high, but they have very small biomasses: the average larva in the population in June 1970 weighed over 3.2 mg d.wt. but in 1971 only 0.45 mg d.wt. The suggestion that 1971 is a year which for certain reasons is a „poorer" year for *Scarabaeidae* is also confirmed by the delayed peaks of numbers and biomass of the population of these insects. Such maxima are observed in 1970 in May-June, but in 1971 not until August. Extracts were made from climatical data for the two study years in an attempt at finding the explanation of this delay. Figure 7 presents the distribution of temperatures and rainfall for 1970 and 1971. A factor which clearly differentiates the two years is the rainfall in the first three months of the season: May, June and July 1971 are distinctly far drier. It would seem probable that in 1971 the soil dried up, forming conditions unfavourable to the development of the population during the first half of that summer. At the same time it was observed that during the second half of that

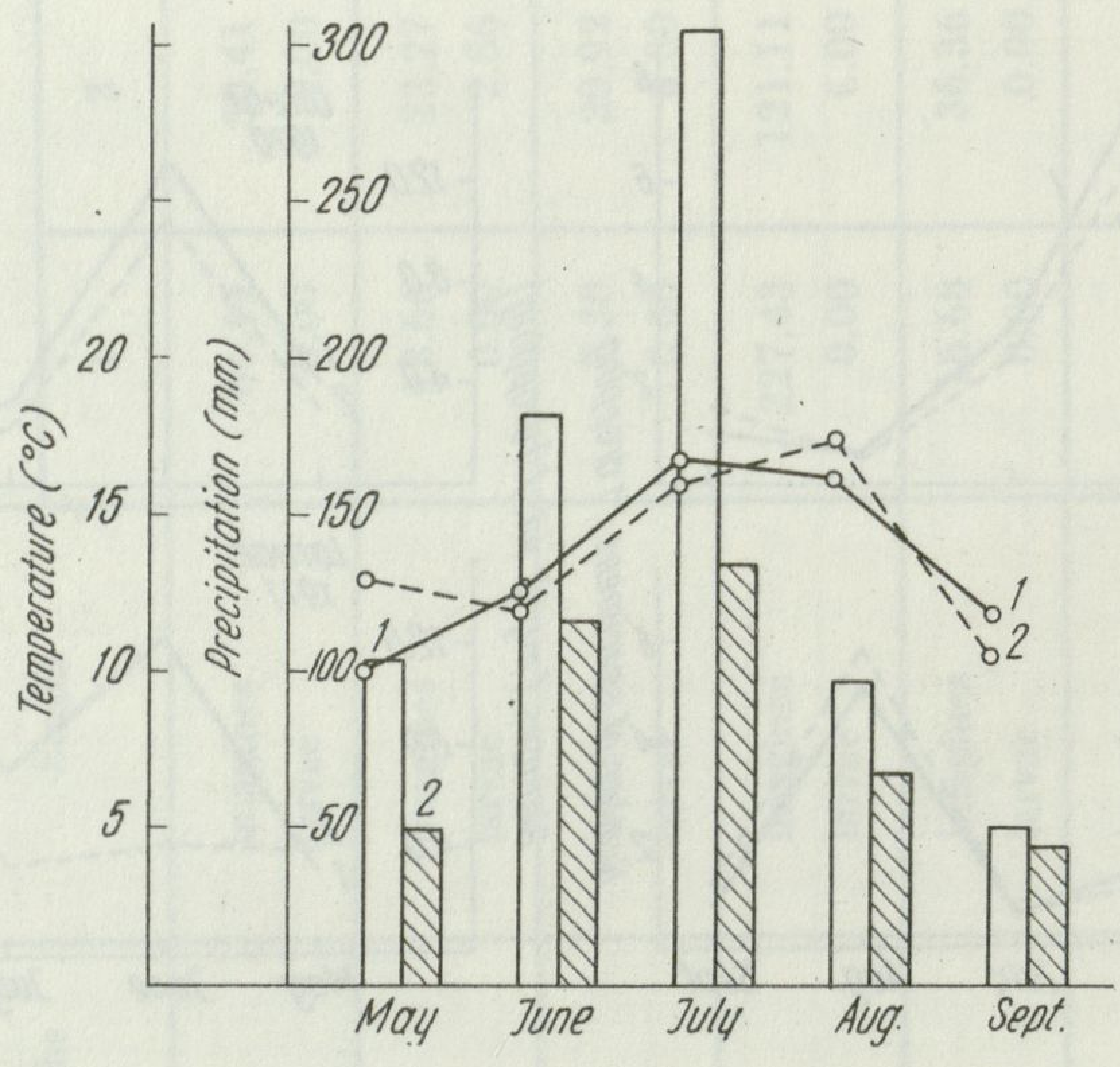

Fig. 7. Soil surface temperatures and rainfall at Jaworki in 1970 and 1971. Author's own data and data from local meteorological station of the Institute of Land Reclamation and Cultivated Lands

Temperature: lines *1* – 1970 and *2* – 1971, rainfall: columns *1* – 1970 and *2* – 1971 summer slightly better temperature conditions occurred than in 1970 and rainfall reached a similar value. There were undoubtedly factors favouring the development of the late summer population of beetles, and this in fact was the case. It would therefore seem that the picture of different development of the scarab populations observed in 1970 and 1971 was due to climatic factors.

3.3. Species composition

Analysis was made of 16 coprophilous species of *Scarabaeidae* in the study pasture. Only a few of these species occurring numerously, and the rest rarely (Tab. V; 3 species, for each of which only 1 individual was caught, were not taken into consideration. These are ***Ontophagus ovatus*** L., ***Oxyomys silvestris*** Scop. and ***Geotrupes*** s. str. ***stercorarius*** L.).

Tab. V. Seasonal changes in species composition of *Scarabaeidae* in 1970 and 1971
Numbers represent the percentages calculated from the number of all beetles caught in a given month

Year	Species	May	June	July	Aug.	Sept.	Average
1970	*A. pusillus* Hbst	38.8	37.2	25.4	5.5	1.4	33.98
	A. ater De Geer	37.0	24.1	16.5	13.2	1.4	27.50
	A. fimetarius L.	1.6	13.2	2.5	39.6	51.1	9.77
	A. heamorrhoidalis L.	0.0	8.7	47.0	11.0	1.4	8.34
	A. luridus F.	9.5	5.1	0.0	0.0	0.0	6.14
	A. sphacelatus Panz.	6.7	4.9	0.0	0.0	0.0	4.82
	O. similis Scr.	1.0	2.8	1.6	0.0	9.5	2.16
	O. fracticornis Preyssl.	1.0	1.0	0.6	2.2	21.4	2.07
	A. depressus Kug.	1.6	1.5	3.8	11.0	0.0	1.94
	A. erraticus L.	2.4	0.5	0.0	2.2	0.0	1.31
	A. rufus Moll	0.0	0.0	2.5	13.2	10.7	1.19
	O. joannae Golj.	0.4	1.0	0.0	0.0	0.0	0.56
	A. rufipes L.	0.0	0.0	0.0	2.2	3.0	0.22
	Total	100	100	100	100	100	100
1971	*A. fimetarius* L.	0.8	9.1	27.4	47.9	55.7	26.09
	A. pusillus Hbst	34.6	25.0	7.5	0.3	0.0	15.41
	O. similis Scr.	1.5	0.8	0.0	25.6	1.4	10.04
	A. sphacelatus Panz.	22.8	0.8	0.0	0.0	5.7	7.67
	A. haemorrhoidalis L.	4.9	23.5	20.5	0.3	0.0	7.08
	O. fracticornis Preyssl.	11.8	3.0	0.0	7.4	1.4	6.97
	A. ater De Geer	5.3	19.7	19.9	0.0	0.0	6.43
	A. depressus Kug.	3.8	10.6	6.8	5.8	0.0	5.55
	A. luridus L.	14.4	2.3	0.0	0.0	0.0	4.84
	A. rufus Moll	0.0	0.0	1.4	3.9	32.9	4.25
	A. erraticus L.	0.0	5.3	5.5	1.9	1.4	2.13
	O. joannae Golj.	0.0	0.0	0.0	5.5	0.0	2.01
	A. rufipes L.	0.0	0.0	11.0	1.3	1.4	1.53
	Total	100	100	100	100	100	100

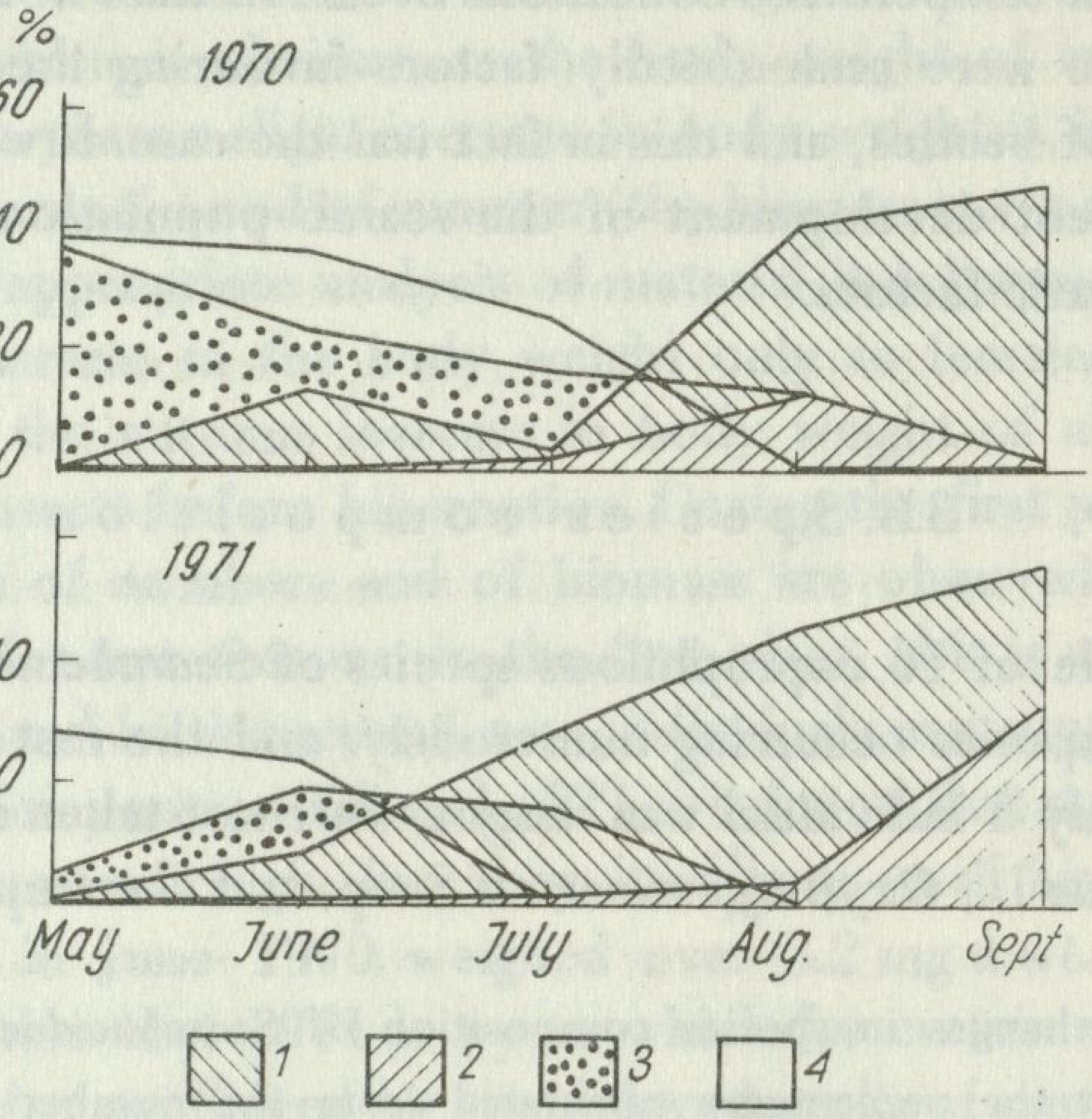

Fig. 8. Seasonal changes in percentages formed by 4 dominants in total numbers of *Scarabaeidae* in 1970 and 1971

1 – *A. fimetarius*, 2 – *A. rufus*, 3 – *A. ater*, 4 – *A. pusillus*

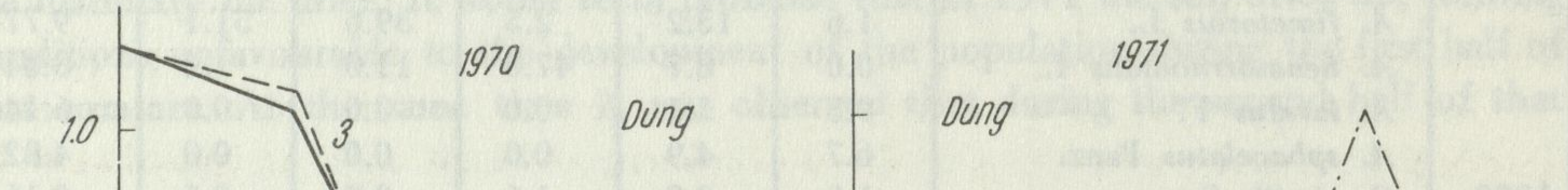

Fig. 9. Seasonal changes in numbers of dominant species of scarabs in two layers of their habitat: in dung and in the soil underneath the dung

Average numbers of imagines per 1 dropping or 1 soil sample. *1 – A. fimetarius, 2 – A. ater, 3 – A. pusillus, 4 – A. haemorrhoidalis, 5 – O. fracticornis*

The quantitative domination of the species is fairly sharply defined, in September the density of the dominant exceeds 50% of the whole population of scarabs, but is less distinct during the first half of summer. Variatrons in numbers of the four dominating species have been plotted on a diagram (Fig. 8). The tendency of these species to more numerous occurrence in different periods of the season is very distinct. *Aphodius pusillus* and *A. ater* must thus be considered as spring species and *A. fimetarius* and *A. rufus* as autumn species. The shifting between the dominance of these two species *A. fimetarius* and *A. pusillus* is particularly sharply defined.

One more attempt was made, in relation to material identified to species, to ascertain whether there is a tendency for some species to concentrate in the excrement itself and for others in the soil under the excrement (Fig. 9). The level of occurrence of the species is far lower in the soil, but almost all species of the beetles occur similarly in the two layers of their habitat. Only *A. haemorrhoidalis* fails to move down into the soil (or if it does so it is in such small numbers that they were not revealed by our methods).

3.4. Utilization of sheep dung by *Scarabaeidae* – transfer of dung into the soil

We attempted to assess the amount of dung carried into the soil by these beetles, using the unpublished results of experiments by S. Jenike-Cianciara (dissertation for master's degree prepared in the Department of Grassland Ecosystems of the Institute of Ecology, Polish Academy of Sciences, 1971). The author bred three species of coprophagous beetles: *Aphodius fimetarius*, *Ontophagus fracticornis* and *Geotrupes stercorarius* (Scriba). The beetles were fed with sheep excrement and kept on clean ignited sand, for which the amount of excrement carried into it was estimated at given intervals of time. The results obtained by Jenike-Cianciara, together with our calculations, are given in Table VI. The calculations made show that beetles carry a total of 12–33 g d.wt. of

Tab. VI. Dung carried into the soil by beetles of the genera *Aphodius* sp. and *Ontophagus* sp.

Species	Dung carried into the soil in mg d.wt./indiv./d*	Average density of individuals of a given genus on the pasture per 1 m^2		Dung carried into the soil in mg d.wt./m^2/season**	
		1970	1971	1970	1971
Aphodius fimetarius	35	6.1	1.9	32 025	9 975
Ontophagus fracticornis	25	0.3	0.5	1 125	1 875
				33 150	11 850

*Unpublished data of S. Jenike-Cianciara (M. Sc. thesis): the author carried out her experiments on the species, her data have been applied in the present paper to groups of species of the same genus.

**It was assumed that the active life of scarabs lasts from May to September, i.e. 150 days.

excrement from 1 m^2 of pasture annually. O l e c h o w i c z (1974) states that 360 g of d.wt. of sheep dung falls annually on 1 m^2 of pastures. Scarabs of the two most numerous genera examined, *Aphodius* and *Ontophagus*, thus carry into the soil from 3–9% of the amount of excrement which falls on the pasture. If individuals from the remaining scanty genera are taken into consideration, we can probably round up the figure obtained to 10%.

4. DISCUSSION

The results presented above describe the occurrence of scarabs on the pasture and one of their functions in the pasture ecosystem – transporting sheep excrement into the soil. The calculated amount of 12–33 g dry weight of excrement carried into the soil from 1 m^2 of pasture when converted to 1 ha gives a fairly imposing figure – 120–330 kg of excrement buried by scarabs in the soil to a depth of several centimetres, i.e. in the layer of growing roots of grasses. According to M y r c h a's (1973) studies on *Copris lunaris* L., after the imagines hatch in the soil more than 80% of the ecrement carried into the soil remains there, i.e. larvae hatching in excrement eat only 20% of its mass. The remainder of the excrement is used by other components of the soil biocenosis. It would appear that "fertilization" of the soil of the pasture is more effective in the case of small beetles carrying small particles of excrement into the soil than in the case of *C. lunaris*, the single "nest" of which contains over 70 g d.wt. of excrement. Small beetles spread excrement more homogeneously, their population constantly moves in both directions: excrement-soil and soil-excrement, and constantly transports small particles of excrement into the soil.

When B r e y m e y e r, J a k u b c z y k and O l e c h o w i c z (in press) examined the development of the microflora of sheep excrement they found that the development of ammonifying bacteria was stimulated by the activity of *Scarabaeidae*, while the development of fungi was inhibited. These authors suggest that fungi are eaten by beetles or that the beetles' activity leads to rapid drying of dung which is unfavourable to fungi. The effect of this selective stimulation of the dvelopment of ammonifying bacteria is probable to accelerate the release, and consequently the circulation of nitrogen in the ecosystem.

According to H o l t e r (1974) the consumption (*C*) by larvae of *Aphodius rufipes* under laboratory conditions is very high and it approximates to 500% of their dry body weight, while the efficiency of assimilation (*A*/*C*) is very low and varies from 7 to 10.4%. Holter has suggested that such a high consumption and low assimilation efficiency in larval *A. rufipes* are related to the trophic conditions in the habitat, which are characterized by a great abundance of food readily available but rapidly disappearing. Under such conditions coprophages can afford, so to say, to be wasteful at further stages of food assimilation, and the low efficiency of assimilation is sufficient for them. If the results of Holter can really be extrapolated to all coprophagous scarabs, the results of B r e y m e y e r, J a k u b c z y k and O l e c h o w i c z (in press) acquire more importance. Scarabs considerably stimulate the development of ammonifying bacteria in dung. Unfortunately, we are not able to do any accurate calculations for our materials. Firstly, Holter examined the larvae and our studies are concentrated upon adult forms. Secondly, the methods we used are not suitable for estimation of the number of larvae, and their densities are certainly underestimated.

The second function of coprophages in the ecosystem is the consumption of excrement and its utilization for the body building and demands of metabolism. In the circulation of matter in a pasture ecosystem this is a role opposite to that described above, in the sense that it leads to slowing down of the rotation of nutrients retained for at least the life span of a generation in their bodies.

Holter (1974) has found that the efficiency of production P/A under laboratory conditions varies from 23–48%. A much higher and probably overestimated P/A ratio was found by Myrcha (1973) for *C. lunaris*; for the larval stages I and II it reaches 80% and for stage III 40–45%. It can probably be concluded from these data that larval scarabs rather economically use the assimilated food for tissue production, the efficiency of production being about 40% (not taking into account the value of 80% found by Myrcha).

In sum in a pasture ecosystem coprophagous scarabs are mainly involved into the mechanisms of matter cycling at two moments. First, when they carry the pieces of dung into the soil. In the pasture under study they can bury in the soil up to 10% of the dung deposited by sheep. Second, when they influence microbiological processes in dung so that the development of ammonifying bacteria is speeded up and in consequence, the releasing of nitrogen too.

5. SUMMARY

Studies were made in 1970 and 1971 of variations in density, biomass and species structure of population of coprophagous beetles (*Scarabaeidae*) occurring in a mountain pasture grazed by sheep (Małe Pieniny mountains). A total of 16 species of beetles were found, chiefly those of the genera *Aphodius* sp. and *Ontophagus* sp. (Tab. V). Both the imagines and larvae of *Scarabaeidae* were observed in sheep excrement and in the 10-centimetre layer of soil beneath the excrement (Fig. 5, 9). It was found that scarabs occupy excrement as early as the first day that it is left on the pasture (Fig. 4, 5, Tab. I–IV). Imagines are numerous on the first few days after excrement is left on the pasture, while the numbers of larvae increase after 5–10 days. The biomass of *Scarabaeidae* was estimated on the basis of correlations calculated for imagines from width of the prothorax and dry weight, and for larvae from the so-called "alcohol" fresh weight and dry weight (Fig. 1–3). Both numbers and biomass exhibit similar variations during the season (Fig. 6). The changes in numbers, and particularly in biomass of *Scarabaeidae* observed in 1971 (Fig. 6), were probably caused by climatic factors. Imagines of the two most numerous genera of *Scarabaeidae* on the pasture, *Aphodius* sp. and *Ontophagus* sp. transport into the soil 12–33 g d.wt. of sheep excrement per 1 m^2 of pasture (Tab. VI), what consists about 10% of excrement left by sheep on the pasture.

6. POLISH SUMMARY (STRESZCZENIE)

W latach 1970 i 1971 badano zmiany zagęszczenia, biomasy i struktury gatunkowej chrząszczy koprofagicznych z rodziny *Scarabaeidae* występujących na pastwisku górskim wypasanym przez owce (Małe Pieniny). Znaleziono 16 gatunków chrząszczy, głównie z rodzajów *Aphodius* sp. i *Ontophagus* sp. (tab. V). Zarówno formy dojrzałe, jak i larwy żukowatych zaobserwowano w kale owczym i w 10-centymetrowej warstwie gleby pod kałem (fig. 5, 9). Stwierdzono, że żukowate zasiedlają fekalia już pierwszego dnia po pozostawieniu nawozu na pastwisku (fig. 4, 5, tab. I–IV). Formy

dojrzałe liczne są w pierwszych dniach po pozostawieniu kału, a liczebność larw wzrasta dopiero po 5–10 dniach. Biomasę żukowatych oceniono na podstawie korelacji obliczonych dla imagines z szerokości przedplecza i suchej masy, a dla larw z tzw. masy świeżej alkoholowej i masy suchej (fig. 1–3). Zarówno liczebność, jak i biomasy wykazują podobną zmienność w sezonie (fig. 6). Sugeruje się, że zmiany w liczebności, a szczególnie w biomasie żukowatych obserwowane w 1971 (fig. 6) spowodowane były czynnikami klimatycznymi. Formy dojrzałe żukowatych z dwu najliczniejszych na badanym pastwisku rodzajów *Aphodius* sp. i *Ontophagus* sp. wnoszą do gleby w czasie sezonu 12–33 g s.m. nawozu owczego z 1 m^2 pastwiska (tab. VI). Ocenia się, że żukowate znoszą do gleby około 3–10% masy nawozu pozostawionego przez owce na pastwisku.

7. REFERENCES

1. B a l t h a s a r U. 1964 – *Aphodiidae* (In: Monographie der *Scarabaeidae* und *Aphodiidae* der palearktischen und orientalischen Region. III) – Verlag der Tschechoslowakischen Akademie der Wissenschaften, Prag, 652 pp.
2. B o r n e m i s s z a G. F. 1969 – A new type of brood care observed in the dung beetle *Oniticellus Cintus* (*Scarabaeidae*) – Pedobiologia, 9: 223–225.
3. B r e y m e y e r A., J a k u b c z y k H., O l e c h o w i c z E. (in press) – Influence of coprophagous arthropods on microorganisms in sheep faeces – laboratory investigation – Bull. Acad. pol. Sci. Cl. II. Sér. Sci. biol. 23.
4. C z e r w i ń s k i Z., K o t o w s k a J., T a t u r A. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). I. Short geobotanical characteristics – Ekol. pol. 22: 475–486.
5. C z e r w i ń s k i Z., T a t u r A. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). II. The soil-geological conditions – Ekol. pol. 22: 487–504.
6. G o l j a n A. 1953 – Studies on Polish beetles of the *Onthophagus ovatus* L. – group with some biological observations on coprophagism – Annls. Mus. zool. pol. 15: 55–88.
7. H o l t e r P. 1973 – A chromic oxide method for measuring consumption in dung-eating *Aphodius* larvae – Oikos, 24: 117–122.
8. H o l t e r P. 1974 – Food utilization of dung-eating *Aphodius* larvae (*Scarabaeidae*) – Oikos, 25: 71–79.
9. M y r c h a A. 1973 – Bioenergetics of the development period of *Copris lunaris* L. – Ekol. pol. 21: 13–35.
10. O l e c h o w i c z E. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). X. Sheep dung and the fauna colonizing it – Ekol. pol. 22: 589–616.
11. R e i t t e r E. 1909 – Fauna germanica. XI – K.G. Lutz' Verlag, Stuttgart, 392 + 80 pp.
12. S c h m i d t G. 1935 – Beiträge zur Biologie der *Aphodinae* (*Coleoptera, Scarabaeidae*) – Stettin. ent. Ztg, 96: 293–350.
13. T r a c z y k T., K o c h e v Kh. 1974 – Analysis of a sheep pasture ecosystem in the Pieniny mountains (the Carpathians). III. Primary production of *Lolio-Cynosuretum* association – Ekol. pol. 22: 505–516.

Paper prepared by J. Stachowiak

AUTHOR'S ADDRESS:
Dr Alicja Breymeyer
Zakład Biocenologii
Instytutu Ekologii PAN
Dziekanów Leśny k. Warszawy
05–150 Łomianki,
Poland.