

EKOLOGIA POLSKA (Ekol. pol.)	26	3	409-427	1978
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ANALYSIS OF CONSUMPTION BY SPIDERS UNDER LABORATORY AND FIELD CONDITIONS*

ABSTRACT: A comparative analysis was made as regards the consumption of eight species of spiders. The regression functions determining the relation between the body weight and daily consumption of an individual allow to state that there may be significant differences in the food demand of particular species. The consumption under laboratory and field conditions (on a meadow *Stellario-Deschampsietum medioeuropaeum*) was compared. The changes in the consumption range were examined when the number of prey supplied increased. Under laboratory conditions the food was most effectively consumed under conditions of food shortage. In the field, the consumption depended on the number of emerging dipterans and not on their mean density.

KEY WORDS: Laboratory experiments, meadow, spiders, consumption, predation, elimination of prey.

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1. INTRODUCTION

Over the past years a lot of data (both laboratory and field) have been obtained on the consumption rate by various species of spiders (Turnbull 1962; Kajak 1967, 1971, Kajak and Stejgwiłło-Laudańska 1968, Miyashita 1968, Hagstrum 1970a, 1970b, Moulder, Reichle and Auerbach 1970, Edgar 1971,

*Praca wykonana w ramach problemu węzłowego nr 09.1.7 („Produktywność ekosystemów trawiastych i leśnych”).

Stejgwiłło-Laudańska 1971, Van Hook 1971, Breymeyer and Józwik 1975, Humphreys 1975, Steigen 1975). Thus, an attempt can be made to compare these results and to estimate the differences in consumption by various species of the same group of arthropods.

The consumption by a population or the trophic level is a significant parameter in the recently increasing number of publications on the energy flow. As it is frequently impossible to obtain each time empirical data on the consumption rate by particular populations, the easiest thing is to introduce appropriate calculations of consumption on the basis of general regression functions describing the relation between the body weight of an individual and the consumption.

Comparisons are made between regression functions calculated for eight species of spiders. The possibility of working out such a general function for spiders is analysed here as well as the possibility of estimating the range of differences as regards the food demand of particular species.

Another important, although controversial, problem is whether the consumption by population in field can be estimated basing on laboratory results. Thus, the field and laboratory results on the food demand of two species of web spiders are compared and the possibilities of increasing that consumption when changing the food supply in the environment are estimated, both under laboratory and field conditions.

Among predatory polyphages the strongest reaction to changes in the number of prey in the environment is the so-called functional response, i.e., changes in the consumption by an individual. Therefore, it is especially important to estimate to what extent the individual consumption by these animals increases.

2. METHODS

Laboratory methods. In order to estimate the consumption the spiders were kept in rearing cages (20 × 20 × 30 cm) made of iron rods and covered with nylon gauze of a mesh size 0.3 mm. About 2–3 small individuals were reared in one cage. The cages were rather big compared to those used by other authors, but this provided room for the spiders to weave webs. The two web species were: *Araneus quadratus* (Clerck) and *Singa heri* (Hahn), and also one of the hunting spiders — *Tibellus maritimus* (Mge.). *S. heri* and *T. maritimus* were given exclusively *Drosophila* sp., *A. quadratus* was also given other species — Auchenorrhyncha (Homoptera) and Acridoidea — of a known weight.

Mean daily temperature in the laboratory ranged from 13 to 27°C.

In the experiment the food supply varied. Detailed data on the number of prey, frequency of feeding and number of replicates for each series are given in Table I. Every two days the numbers of prey not consumed by the spiders were checked, dead individuals and other food remains were dried and weighed, and a fresh supply of prey matching the initial one was provided.

In all the experiments where the spiders were fed with *Drosophila* sp. there was a so-called control experiment, i.e., the same number of *Drosophila* sp. was placed simultaneously in analogous cages without spiders. This material was used for estimating the weight of food supplied, and also to determine the possible losses that could have taken place during feeding or due to natural mortality of flies.

The rearing of *Singa heri* covered all the development stages following the dispersion of individuals out of cocoons. This experiment lasted between April and October (in 1971 and

Table I. Scheme of feeding experiments

Species	Period of life cycle and average weight (mg f. wt)	Period	Number and type of prey supplied	Daily prey supply per individual (mg d. wt)	Number of replicates
<i>Singa heri</i>	experiment I: adult females 6.5-12	23 June-2 Aug.	15 <i>Drosophila</i> sp. 30 <i>Drosophila</i> sp.	0.2-2.4	9 10
	experiment II: instars 1.0-1.5	3 Aug.-28 Oct.	15 <i>Drosophila</i> sp. 30 <i>Drosophila</i> sp.	0.05-1.6	7 9
	experiment III: instars and adult females 4.0-16	24 April-11 July	15 <i>Drosophila</i> sp. 30 <i>Drosophila</i> sp. 40 <i>Drosophila</i> sp. 50 <i>Drosophila</i> sp.	0.2-3.5	5 5 5 2
<i>Tibellus maritimus</i>	instars 0.3-2.3	24 July-16 Sept.	15 <i>Drosophila</i> sp. 30 <i>Drosophila</i> sp.	0.05-0.9	8 8
<i>Araneus quadratus</i>	subadult and adult females 25-300	18 July-30 Sept.	5 <i>Drosophila</i> sp. 10 <i>Drosophila</i> sp. 15 <i>Drosophila</i> sp. 3 Auchenorrhyncha (Hom.) 6 Auchenorrhyncha (Hom.) 9 Auchenorrhyncha (Hom.) 3 Acridoidea 6 Acridoidea 9 Acridoidea	0.17-287	4 4 4 4 4 4 4 4 4

1972), i.e., over the period when this species is active under field conditions. The other species of spiders were reared for a shorter time, and these were treated as supplementary – *Araneus quadratus* starting from the two last instars up to adult females; *Tibellus maritimus* – only young individuals. The spiders were weighed in weekly intervals and fresh weight was estimated.

The consumption by spiders was determined as:

$$\text{consumption} = \text{weight of food supply} - \left(\begin{array}{l} \text{weight of} \\ \text{not consumed} \\ \text{insects} \end{array} + \begin{array}{l} \text{weight} \\ \text{of} \\ \text{remains} \end{array} \right)$$

In comparing the field and laboratory results the weight of prey killed was used instead of the consumption. It is a better measure of the effect of predator population on prey and also easier to obtain in field:

$$\text{weight of prey killed} = \text{consumption} + \text{weight of food remains}$$

Field methods. The field data that have been used for comparison with laboratory results were obtained over four seasons from 1965 to 1968. The studies were conducted on a meadow *Stellario-Deschampsietum medioeuropaeum* (Traczyk 1966). The material previously published in other papers (Kajak 1967, 1971, Kajak and Olechowicz 1969) was used in these comparisons; these papers included also a detailed description of methods for estimating the weight of prey caught in webs. The method consisted of marking 50–100 webs on the meadow and of recording twice a day the number of prey in the webs. At the second check the food in the webs was taken and sorted in the laboratory. The dipterans – the most abundant food component – were identified to their families. Parallel studies were conducted on the production and density of adult dipterans in the environment (Olechowicz 1971). They provided data on the weight of dipterans that could be found in webs.

The density of spiders was estimated by the quadrat samples, in which the spiders of the field layer were counted on areas covered by the frame 50 × 50 cm. Each time, i.e., once a week, 10 such samples were taken and the webs were controlled equally frequently.

3. CONSUMPTION AND THE BODY WEIGHT OF AN INDIVIDUAL

At a sufficient food supply in the environment the amount of food consumed depends first of all on the size of an individual which is the result of a generally valid relation between the body weight and the metabolism rate (Zeuthen 1953, Engelmann 1961, Kleiber 1961). Thus, when comparing the consumption by various species this relation had to be firstly considered. For each of the species compared there were functions describing the relations between the mean body weight of an individual in a given stage and the amount of food consumed per day. The following material was used:

1. Published data showing the changes in consumption in the course of life cycle of four species: *Linyphia triangularis* Cl. (Turnbull 1962), *Tarentula kochii* (Keys.) (Hagstrum 1970a, 1970b), *Pardosa lugubris* (Walck.) (Edgar 1971), *Trochosa ruricola* (De Geer) (Stejgwiłło-Laudańska 1971). These data allowed to determine functions describing the relation between the body weight and consumption.

2. Own material from the already mentioned feeding experiments of three species of spiders: *A. quadratus*, *S. heri*, *T. maritimus*.

3. Regression functions showing the relation between consumption and body weight given in papers published, namely the function for *Geolycosa godeffroyi* (l. Koch) (H u m p h r e y s 1975) and suggested by Reichle (1968) on the basis of material of 11 species of arthropods, including spiders.

The consumption depends very much not only on the size of an individual, but also on the amount of food available in the environment, on the development stage and mobility of the predator, and on climatic conditions influencing the activity of animals.

To estimate the relation between consumption and the body weight of a predator the care was taken to diminish the effect of other factors on the results. Thus, only these experiments where the amount of food was not limited, i.e., there was no mortality due to food deficiency, were taken into account. In these cases only some of the prey were caught by spiders. Also the females after forming cocoons were not taken into account as their food demand may be unproportionally low as compared with other stages (Miyashita 1968, Steigen 1975); adult males were excluded for the same reasons¹.

The regression functions expressing the relation between the weight of an individual and the daily food consumption by eight species of spiders examined, are given in Table II. All these relations are statistically highly significant. Snedecor *F*-test, based on variance analysis, was used to compare differences in the course of successive pairs of functions by determining the significance level of differences in the slope of curves (comparison of parameter *B*) and at the crossing point of regression lines with *y* axis (comparison of parameter *A*). In this case, parameter *A* informs about the amount of food consumed by an individual when it weighs 1 mg fresh weight, whereas parameter *B* – about the rate of increase of the amount of food consumed as the individual gains weight. Each with each were compared. When comparing parameters *A* and *B*, in functions from own calculations, the variance analysis based on *F* criterion was used (Table III), whereas when comparing functions from publications (Reichle 1968, Humphreys 1975) the Student *t*-test was used (Table IV).

It has been observed that the differences among species as regards the amount of food consumed are considerable. At the same weight of an individual the mean consumption may differ by several tens of times. The differences were greater among the values of parameter *A* than those of parameter *B*; the differences in the latter were insignificant for the majority of tests (Tables III, IV). The maximum difference in the values of parameter *A* was 23-fold (between the consumption of species *Geolycosa godeffroyi* and *Tarentula kochii*).

Regression lines showing the relation between the body weight and consumption of an individual can be divided into three groups, within which there are not any significant differences in the values of parameters *A* and *B*.

The group of large species (I) – *A. quadratus*, *T. ruricola*, *G. godeffroyi* – is distinguished by its greatest food demand at a given body weight (Tables III, IV, Fig. 1) and the highest production rate. According to published data (Kajak 1971, Stejgwiłło-Laudańska 1971, Humphreys 1975) it can be assumed that mean daily increments in the weight of an individual are over 0.5 mg f. wt for the species of this group. The arthropod species described by Reichle (1968) should be also included to this group.

Differences in the consumption of species belonging to the other two groups (II, III) are smaller than for large species. These species have similar increments, much smaller than in

¹Regression function for *G. godeffroyi* and *T. kochii* was based on material for both sexes.

Table II. Regression functions between body weight (w – mg f. wt) and consumption (C – mg d. wt · ind.⁻¹ · day⁻¹)

Species	Function $C = Aw^B$	Standard error of parameter		F-test	d.f.**	Author
		A	B			
<i>Araneus quadratus</i>	$C = 0.20w^{0.71}$	0.4928	0.1272	31.00	69	A. Kajak (unpublished data)
<i>Trochosa ruricola</i>	$C = 0.26w^{0.43}$	0.2243	0.070	37.93	8	Stejgwiłło-Laudańska (1971)
<i>Geolycosa godeffroyi</i>	$C = 0.13w^{0.76*}$		0.0085		14	Humphreys (1975)
<i>Linyphia triangularis</i>	$C = 0.05w^{0.87}$	0.0715	0.040	473.8	12	Turnbull (1962)
<i>Singa heri</i>	$C = 0.06w^{0.56}$	0.1720	0.1216	21.23	48	A. Kajak (unpublished data)
<i>Pardosa lugubris</i>	$C = 0.02w^{0.73}$	0.2005	0.1142	40.91	10	Edgar (1971)
<i>Tarentula kochii</i>	$C = 0.01w^{0.84}$	0.1457	0.0542	239.05	9	Hagstrum (1970a)
11 arthropod species	$C = 0.06w^{0.68*}$					Reichle (1968)
<i>Tibellus maritimus</i>	$C = 0.03w^{1.57}$	0.1644	0.2872	29.78	14	A. Kajak (unpublished data)

* w – in mg d. wt. **d.f. – degree of freedom.

Table III. Comparison of consumption of several spider species by *F*-test
 Figures underlined = significant differences ($p < 0.01$). Species belonging to the same group are in frames. *d.f.* – degree of freedom

Species compared		Regression function parameters compared			
		F_A	<i>d.f.</i>	F_B	<i>d.f.</i>
<i>A. quadratus</i>	<i>S. heri</i>	<u>31.76</u>	1, 116	0.70	1, 115
	<i>L. triangularis</i>	<u>8.86</u>	1, 82	0.67	1, 81
	<i>T. kochii</i>	<u>56.98</u>	1, 77	0.27	1, 76
	<i>T. ruricola</i>	4.00	1, 76	1.33	1, 75
	<i>P. lugubris</i>	<u>34.43</u>	1, 78	0.01	1, 77
	<i>T. maritimus</i>	<u>8.32</u>	1, 80	4.05	1, 79
<i>S. heri</i>	<i>L. triangularis</i>	0.82	1, 61	2.80	1, 60
	<i>T. kochii</i>	<u>7.73</u>	1, 16	1.38	1, 15
	<i>T. ruricola</i>	<u>12.62</u>	1, 55	0.32	1, 54
	<i>P. lugubris</i>	<u>7.22</u>	1, 57	0.49	1, 56
	<i>T. maritimus</i>	1.90	1, 59	6.02	1, 58
<i>L. triangularis</i>	<i>T. kochii</i>	<u>102.94</u>	1, 22	<u>11.94</u>	1, 21
	<i>T. maritimus</i>	<u>17.37</u>	1, 25	<u>19.00</u>	1, 24
<i>T. kochii</i>	<i>T. ruricola</i>	<u>121.12</u>	1, 16	<u>21.23</u>	1, 15
	<i>P. lugubris</i>	3.41	1, 18	0.71	1, 17
	<i>T. maritimus</i>	<u>12.82</u>	1, 20	7.93	1, 19

Table IV. Comparison of consumption of several arthropod species using the Student *t*-test between parameters (*A*, *B*) of the function $C = Aw^B$ for pairs of species

C consumption (mg d. wt · ind.⁻¹ · day⁻¹), *w* – fresh body weight (mg). – Comparison regressions presented by Reichle (1968) and Humphreys (1975) were recalculated, *w* was expressed in fresh weight assuming 67% of water content in an animal. Figures underlined = significant differences ($p < 0.01$)

Species	<i>G. godeffroyi</i>		Several arthropod species	
	t_A	t_B	t_A	t_B
<i>A. quadratus</i>	0.82	0.042	0.86	0.22
<i>T. ruricola</i>	0.73	4.72	2.97	3.56
<i>S. heri</i>	<u>6.25</u>	<u>0.001</u>	2.68	0.58
<i>L. triangularis</i>	<u>28.80</u>	2.69	3.07	<u>4.72</u>
<i>P. lugubris</i>	<u>13.19</u>	0.27	9.05	<u>0.44</u>
<i>T. kochii</i>	<u>21.59</u>	0.82	<u>15.90</u>	2.93
<i>T. maritimus</i>	<u>13.19</u>	2.81	<u>8.14</u>	3.09

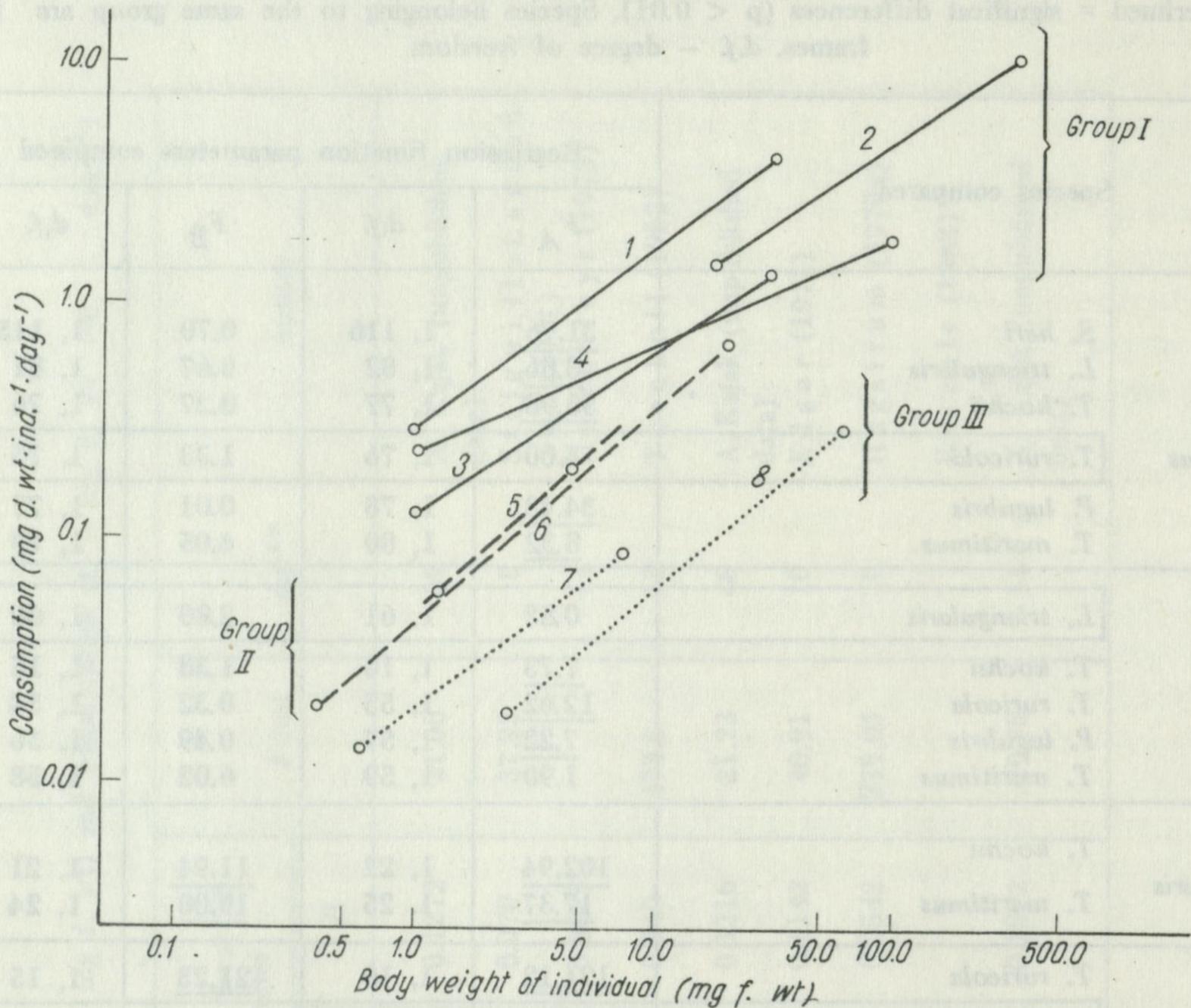


Fig. 1. Regression lines expressing the relation between the body weight of an individual and consumption. Species of group I: 1 — *Geolycosa godeffroyi*, 2 — *Araneus quadratus*, 3 — different species of arthropods, 4 — *Trochosa ruricola*; species of group II: 5 — *Singa heri*, 6 — *Linyphia triangularis*; species of group III: 7 — *Pardosa lugubris*, 8 — *Tarentula kochii*

group I where they ranged from 0.05 to 0.20 mg f. wt·ind.⁻¹·day⁻¹ (Turnbull 1962, Hagstrum 1970a, Edgar 1971, Kajak 1971). Within groups II and III, with species having small increments, a greater food demand was displayed by univoltine and web spinning species (*L. triangularis*, *S. heri*) than by the multivoltine and wandering species (*P. lugubris*, *T. kochii*).

In the comparisons of various species *T. maritimus* has not been taken into account as the corresponding regression function for this species slopes quite differently from others (Tables III, IV). This is probably, because young individuals of this species were reared only.

The comparisons show that even consumption by related species displays also considerable differences. One of the criteria for finding whether regression functions for one species can be used for another is the weight increment rate. Species with high increments had a much higher consumption at the same weight of an individual than other species. But this was not always a sufficient criterion. In the group of species with similar increments there were also significant differences in consumption, although smaller (Table III). At similar increments the consumption of univoltine species was higher than of multivoltine ones.

4. COMPARISON OF LABORATORY AND FIELD DATA ON CONSUMPTION

Laboratory and field measurements are rarely being collected and it is still a matter of discussion whether laboratory results can be transposed into field conditions. The regression functions between the body weight of an individual and the mean weight of prey killed daily of two species of web spiders – *A. quadratus* and *S. heri* – are compared on the basis of field and laboratory material (Table V). An analysis of the significance of differences in parameters *A* and *B* of functions on the basis of *F*-test was made. In these comparisons the entire experimental material was considered, i.e., both series where the amount of food supplied was insufficient, and where there was an excess of food.

Table V. Comparison of field and laboratory regression functions
 w – mg f. wt, y – d. wt · ind⁻¹ · day⁻¹ Figures underlined = significant differences ($p < 0.01$)

Species	Function between body wt (w) and prey killed (y) ($y = Aw^B$)		Food supply (mg d wt · ind. ⁻¹ · day ⁻¹)	Regression parameters compared by <i>F</i> -test			
	field	laboratory		F_A	<i>d.f.</i>	F_B	<i>d.f.</i>
<i>A. quadratus</i>	$y = 0.32w^{0.538}$	$y = 0.21w^{0.69}$	0.17–287	0.58	0.108	1.12	1.107
		$y = 0.72w^{0.76}$	0.40–0.72	<u>14.57</u>	1.43	3.84	1.42
<i>S. heri</i>	$y = 0.02w^{1.15}$	$y = 0.10w^{0.70}$	0.40–1.11	<u>27.70</u>	1.54	5.17	1.53

Field and laboratory results were consistent in the case of *A. quadratus* (Table V). In the feeding experiments with *A. quadratus* the food was supplied in very small amounts (0.17 mg d. wt · ind.⁻¹ · day⁻¹) up to amounts considerably exceeding the daily food demand (287 mg d. wt · ind.⁻¹ · day⁻¹) (Table VI). High differentiation of the amount of food provided, obviously imitates well the field conditions as both field and laboratory results approximated. Whereas the differences in the course of laboratory and field regression functions for *S. heri* were of the same order as in the consumption by species from different groups (Tables III, IV). The amount of food supplied for *S. heri* was less differentiated than for *A. quadratus* (0.05–3.5 mg d. wt · ind.⁻¹ · day⁻¹), and also in all series the food was provided in excess as the spiders consumed less than 50% of prey. The results were closer to the field ones when calculating the regression function on a series of experiments with the smallest feeding level (0.05–0.8 mg d. wt · ind.⁻¹ · day⁻¹) (Table V).

These results seem to point that the similarity or divergence between laboratory and field results depend considerably upon the food rationing. A limited amount of food or considerably differentiated amounts of food allow results approximating to the field to be obtained.

Table VI. Changes in daily consumption and efficiency of food utilization at increasing food supply (d. wt)

Singa heri I, II, III – see Table I

Species	Food supply		Consumption		Efficiency of utilization: consumption/food supply (%)
	mg ind. ⁻¹	mg · mg ⁻¹	mg · ind. ⁻¹	mg · mg ⁻¹	
<i>Araneus quadratus</i>	0.26	0.0032	0.25 ± 0.03	0.0030	96
	0.60	0.01	0.43 ± 0.02	0.0048	72
	7.72	0.63	1.31 ± 0.36	0.11	17
	15.6	1.39	2.88 ± 0.70	0.26	18
	19.6	1.38	1.95 ± 0.36	0.14	10
	97.8	3.01	6.78 ± 1.07	0.21	7
	206.4	3.54	13.24 ± 2.20	0.23	6
<i>Tibellus maritimus</i>	0.04	0.17	0.02 ± 0.001	0.08	50
	0.07	0.33	0.02 ± 0.003	0.10	29
	0.35	0.38	0.08 ± 0.01	0.09	23
	0.67	0.84	0.14 ± 0.02	0.18	21
<i>Singa heri</i> I	0.48	0.17	0.17 ± 0.02	0.06	35
	0.80	0.29	0.22 ± 0.03	0.08	28
	1.12	0.34	0.22 ± 0.03	0.07	20
	1.93	0.77	0.36 ± 0.06	0.14	19
<i>Singa heri</i> II	0.12	0.30	0.03 ± 0.04	0.08	25
	0.29	0.71	0.06 ± 0.02	0.15	24
	0.50	1.16	0.14 ± 0.04	0.33	28
	0.67	1.76	0.15 ± 0.03	0.39	22
	1.24	3.65	0.19 ± 0.03	0.56	15
<i>Singa heri</i> III	0.16	0.05	0.11 ± 0.003	0.04	69
	0.44	0.26	0.23 ± 0.02	0.14	52
	0.79	0.38	0.34 ± 0.04	0.16	43
	1.32	0.57	0.41 ± 0.06	0.18	31

5. CONSUMPTION AND THE FOOD SUPPLY

Spiders as polyphages of a relatively long life-span display some characteristic independence of prey population dynamics. Changes in the density of predator population due to food supply are delayed. The only immediate response to the increased amount of food in the environment is higher consumption by particular individuals (functional response) and possible concentration of individuals in areas with higher food supply. Thus the ability of predator population to reduce the increasing number of prey depends considerably on the rate of increase of the individual consumption rate at a given increase in the number of prey.

The laboratory experiments were used to estimate the changes in consumption by an individual with the increasing food supply and the efficiency of food utilization.

The ratio of consumption to the amount of food supplied expresses the efficiency of food utilization.

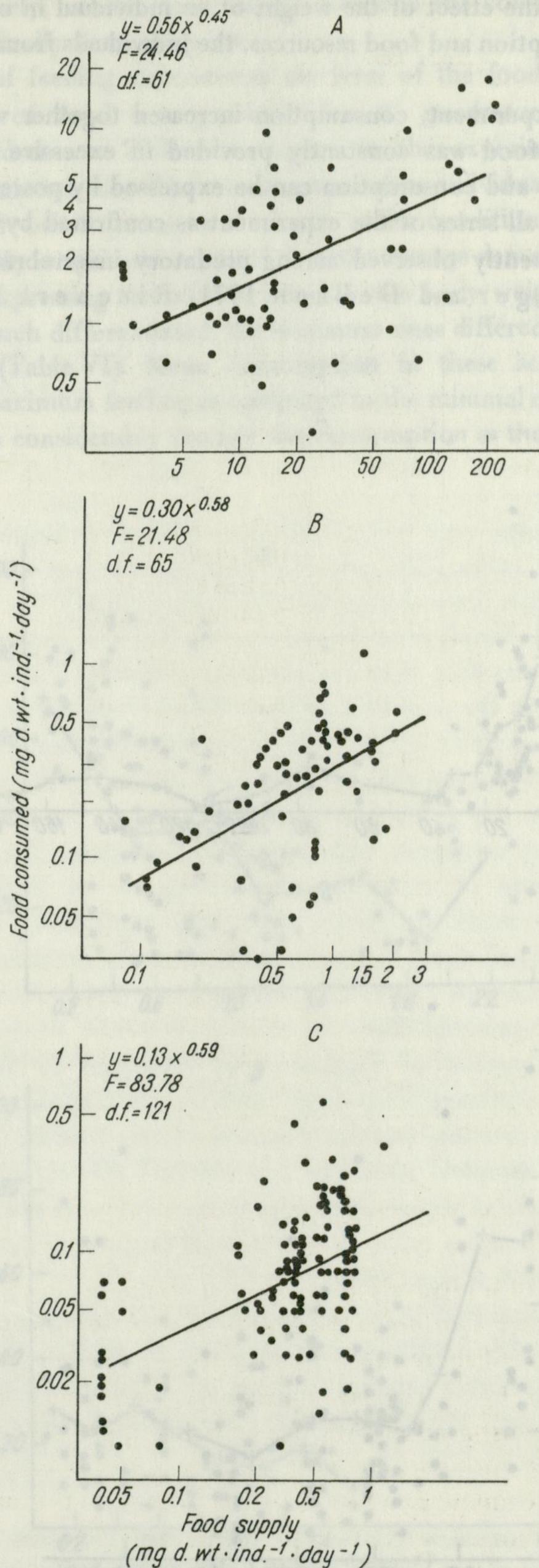


Fig. 2. Relation between the amount of food supplied and consumption
 A – *Araneus quadratus*, B – *Singa heri*, C – *Tibellus maritimus*, d.f. – degree of freedom

In order to eliminate the effect of the weight of an individual in our considerations of the relation between consumption and food resources, the individuals from various size classes were examined separately.

In all series of the experiment, consumption increased together with the increasing food supply, even when the food was constantly provided in excessive quantities. The relation between the food supply and consumption can be expressed by power functions (Fig. 2). This relation is significant in all series of the experiment as confirmed by *F*-test. This is a type of functional reaction frequently observed among predatory invertebrates (Holling 1965, Huffaker, Messenger and DeBach 1971, Riechert 1974, Kiritani and

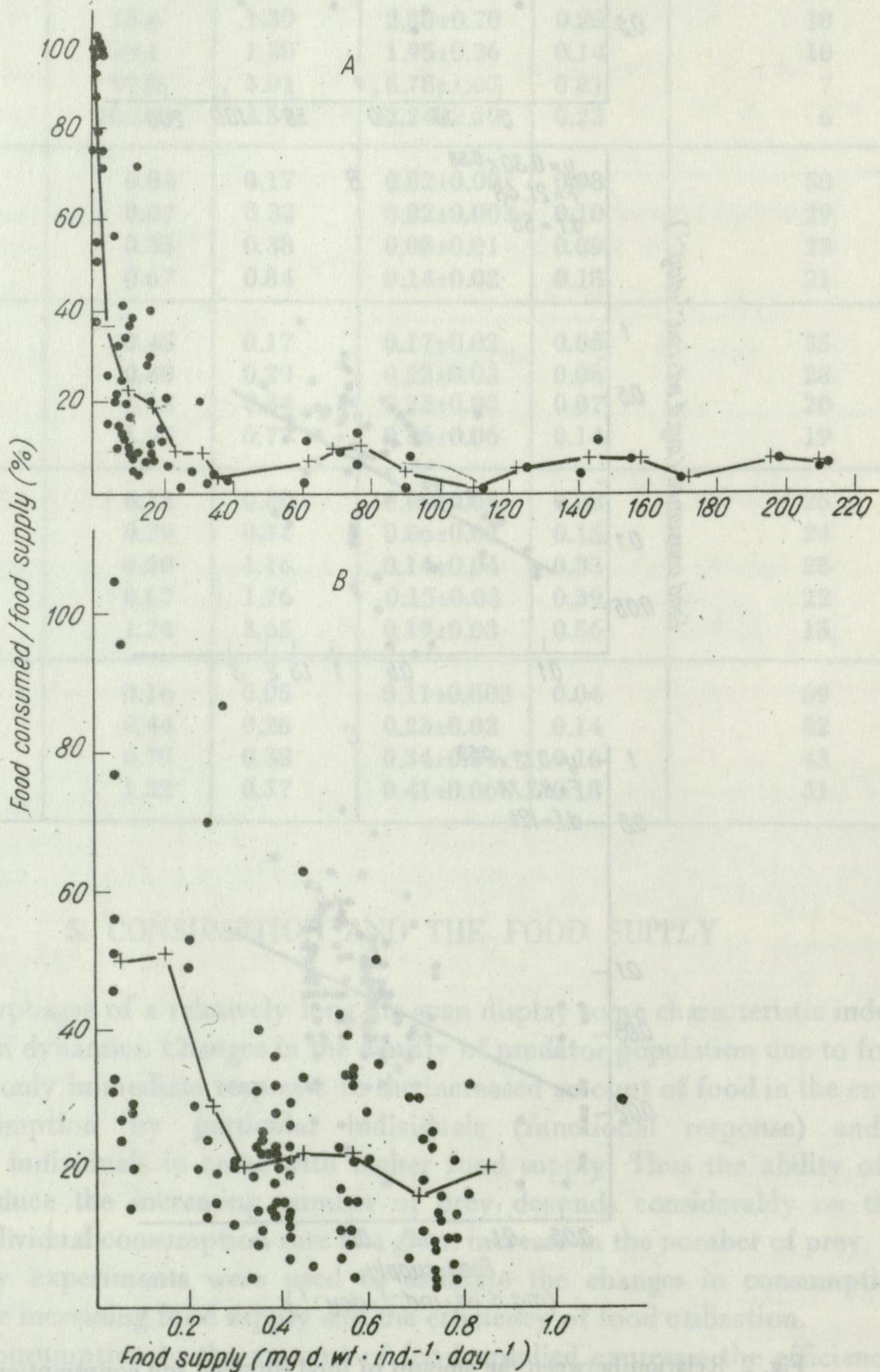


Fig. 3. Extent of food utilization at its different doses

A — *Araneus quadratus*, B — *Tibellus maritimus*

K a k i y a 1975). Namely, as the food supply increases the consumption of an individual increases, but in the gradually decreasing rate.

In particular series of feeding experiments the level of the food supply varied. The most differentiated amount of food was provided for *A. quadratus* (Table VI). The mean amount of food provided was 790 times higher in the experiment kept on maximum feeding level than in minimum one. The consumption of an individual increased then 50 times.

The experiments with other species were usually under conditions of food excess. That is, more food per mg of body weight was supplied than the average demand calculated on the basis of regression function expressing the relation between the body weight and consumption. The food rations were not much differentiated, the minimum ones differed from the maximum ones usually several times (Table VI). Mean consumption in these series of experiments was 2.3–7 times higher at maximum feeding as compared to the minimal one.

Although spiders can considerably modify the consumption as the food supply changes, the

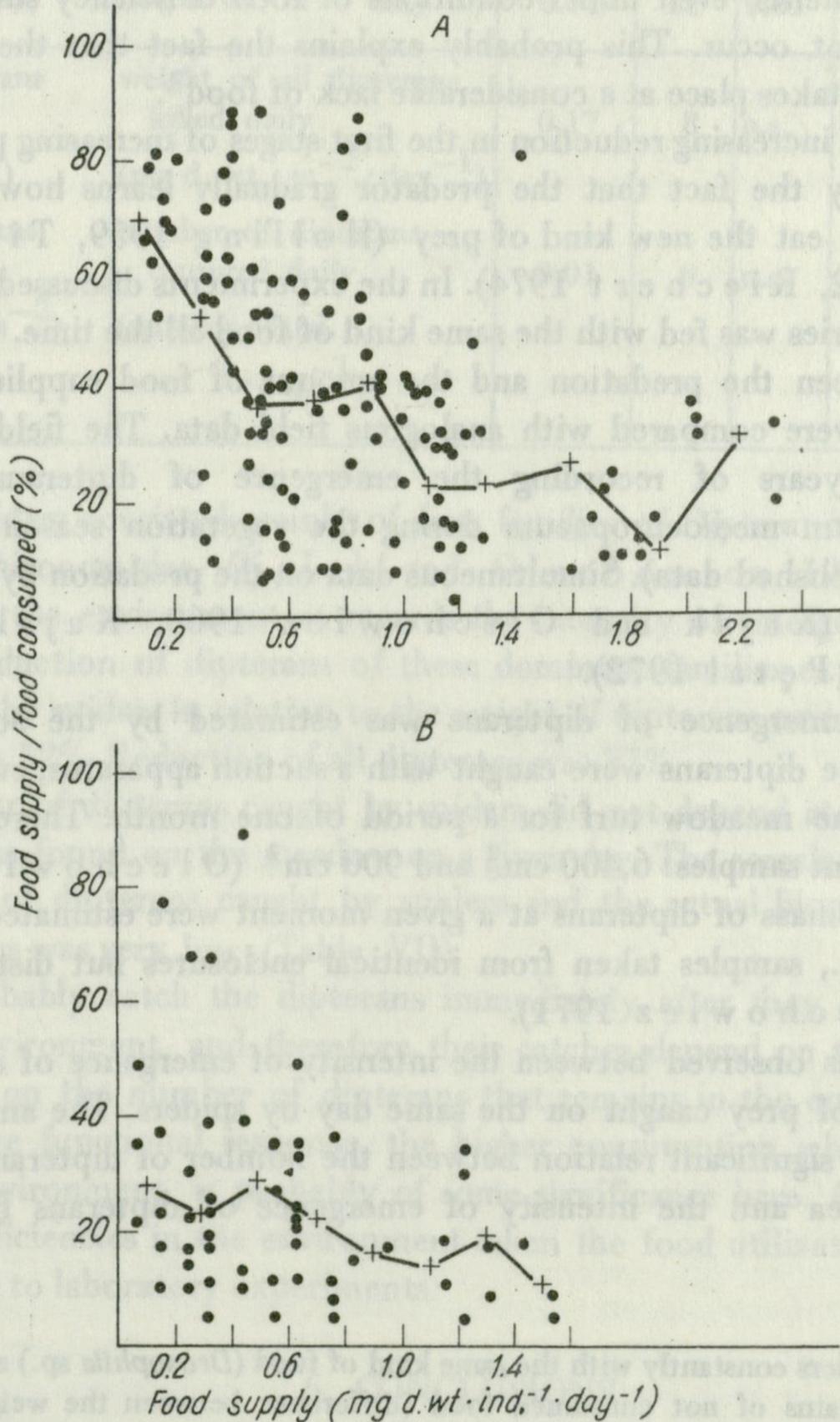


Fig. 4. Efficiency of food utilization by *Singa heri* at different food supply

A – feeding experiments No. I, III, large individuals of a weight 4–16 mg f. wt, B – feeding experiment No. II, small individuals of a weight 1.0–1.5 mg f. wt

consumption increase does not keep pace with the increasing amount of food provided and gradually the efficiency of food utilization decreases.

An especially high utilization of food was observed at food deficiency where the mean food supply did not exceed 0.05 mg/mg body weight of spider per day. The utilization of food was very high, 70–100% (Fig. 2). But also when the food was given in excess the mean utilization of food depended on the amount of food supply. At doses of an order 0.1–0.5 mg/mg the mean utilization was some 30%. At doses from 0.61 to 1 mg/mg the food provided was utilized in some 20% and at doses over 1 mg/mg it ranged from 6 to 28%.

Thus, in these experiments the utilization of prey distinctly decreased as the food conditions improved (Figs. 3, 4, Table VI).

Dąbrowska-Prot, Łuczak and Tarwid (1968) have observed in a field experiment, under conditions of very limited food resources, a gradually increasing predation as the number of prey increased till the optimum of the relation prey (mosquitoes)-predator (spiders) was obtained (1.5–2 mosquitoes per one predator), at which there was maximum predation observed.

Here, in the experiments, even under conditions of food deficiency such small number of prey per spider did not occur. This probably explains the fact that the predation did not increase as it obviously takes place at a considerable lack of food².

The phenomenon of increasing reduction in the first stages of increasing population numbers is usually explained by the fact that the predator gradually learns how to catch the prey efficiently and how to eat the new kind of prey (Holling 1959, Tinbergen 1960, Kiritani et al. 1972, Riechert 1974). In the experiments discussed here this could not be important as each series was fed with the same kind of food all the time.

The relations between the predation and the amount of food supplied, obtained in the feeding experiments, were compared with analogous field data. The field material had been obtained from two years of recording the emergence of dipterans on the meadow *Stellario-Deschampsietum medioeuropaeum* during the vegetation season (Olechowicz 1970, 1971 and unpublished data). Simultaneous data on the predation by web spiders on this area were also used (Kajak and Olechowicz 1969, Kajak 1971, Kajak, Olechowicz and Pełtal 1972).

The intensity of emergence of dipterans was estimated by the so-called method of permanent samples. The dipterans were caught with a suction apparatus, every 1–3 days; from enclosures dug into the meadow turf for a period of one month. There were two sizes of enclosures for permanent samples: 6,400 cm² and 900 cm² (Olechowicz 1971).

The density and biomass of dipterans at a given moment were estimated using the so-called temporary samples, i.e., samples taken from identical enclosures but distributed only at the time of sampling (Olechowicz 1971).

A close relation was observed between the intensity of emergence of dipterans on a given day and the number of prey caught on the same day by spiders. The analysis of correlation showed that there is a significant relation between the number of dipterans caught in webs of spiders on a given area and the intensity of emergence of dipterans from the same area (Table VII).

²When feeding the spiders constantly with the same kind of food (*Drosophila* sp.) and under conditions of food abundance the remains of not consumed food (difference between the weight of prey killed and consumption) were 15–37% of the weight of prey killed, independently of the food supply. As the proportion of food remains ranged to some extent, independently of the food supply, the efficiency of food utilization may be treated as an index of the predation observed (ratio of prey killed to their total number in the environment).

Table VII. Correlation between food supply and food killed by web spiders in Stellario-Deschampsietum medioeuropaeum community

n.s. — not significant

Parameter x	Parameter y	Correlation coefficient (r)	$d.f.$	p	Kind of samples used to estimate the prey number
Weight of all dipterans emerging daily (mg d. wt $\cdot m^{-2} \cdot day^{-1}$)	weight of all dipterans killed daily (mg d. wt $\cdot m^{-2} \cdot day^{-1}$)	0.71	14	0.01	large, permanent samples
		0.66	11	0.05	small, permanent samples
Weight of dominant dipteran species emerging daily (mg d. wt $\cdot m^{-2} \cdot day^{-1}$)	weight of dominant dipteran species killed (mg d. wt $\cdot m^{-2} \cdot day^{-1}$)	0.71	11	0.01	small, permanent samples
Biomass of dipterans (mg d. wt $\cdot m^{-2}$)	weight of all dipterans killed daily (mg d. wt $\cdot m^{-2} \cdot day^{-1}$)	0.17	8	n.s.	large, temporary samples
Density of dipterans (number of ind. $\cdot m^{-2}$)	number of dipterans captured daily (number of ind. $\cdot m^{-2} \cdot day^{-1}$)	-0.01	9	n.s.	large, temporary samples

The food of spiders consisted mainly of four families of Diptera: Sciaridae, Cecidomyidae, Bibionidae and Chironomidae (Kajak and Olechowicz 1969). The same families dominated also in the environment as regards the intensity of emergence (Olechowicz 1971). Average reduction of dipterans of these dominant families expressed as the weight of individuals caught by spiders in relation to the weight of dipterans emerging from the same area over the season was 52%. Reduction of all dipterans was 37%.

Still, the number of dipterans caught by spiders did not depend at all upon the biomass or density of dipterans found on the meadow on a given day. The correlation coefficient between the daily number of dipterans caught by spiders and the actual biomass, and even more the density, of dipterans was very low (Table VII).

The spiders probably catch the dipterans immediately after they emerge, when they just enter the given environment, and therefore their catches depend on the number of emerging dipterans and not on the number of dipterans that remains in the environment. The already discussed immediate functional response, the higher consumption when the number of prey increases in the environment, is probably of some significance here. Also, there are probably periodical food deficiencies in the environment when the food utilization (predation) may be very high according to laboratory experiments.

6. CONCLUSIONS

1. There are considerable differences in the food demand of different species of spiders, which have been shown by analyses of power functions describing the relation between the weight of an individual and the consumption. Thus, the calculation of consumption by a

population on the basis of the function determined for another species may be biased. Consumption by individuals of the same weight but from different species may differ up to several tens.

2. Functional response of spiders, i.e., increase of individual consumption when the food supply increases, may be quite high. In the presented feeding experiments it increases several tens of times when compared with spiders kept under conditions of food shortage and food excess. Even when the excess of food is maintained constantly, a further increase of the food supply results in 2.3–7-fold increase of consumption. The relation between food supply and consumption takes the form of a power function.

3. Under field conditions a significant relation has been observed between the food supply, expressed by the emergence intensity of dipterans, and the consumption by spiders. But there is no relation between the current biomass of these insects and the consumption by spiders. This seems to prove that the predation by spiders occurs immediately after the emergence of dipterans.

The author wishes to acknowledge Dr. T. Wierzbowska for helping in statistical elaboration of the data, H. Pielatowa, M.Sc., for the indispensable calculations on a digital computer, Dr. E. Olechowicz and Dr. B. Stejgwiłło-Laudańska for making available their unpublished data. Special gratitude is given to Mrs H. Łuczak for making the care of spider cultures and valuable help in processing the data.

7. SUMMARY

The regression functions, determining the relation between the body weight and consumption by spiders, were compared. The functions were determined on the basis of own material on species: *Araneus quadratus*, *Singa heri*, *Tibellus maritimus* (Table I) or on the basis of literature data on *Linyphia triangularis* (Turnbull 1962), *Tarentula kochii* (Hagstrum 1970a), *Pardosa lugubris* (Edgar 1971), *Trochosa ruricola* (Stejgwiłło-Laudańska 1971).

The group of species with the highest increment of body weight (over 0.5 mg f. wt per individual per day) has also a greater food demand (Fig. 1, Table II). The differences are statistically significant as it has been confirmed by comparing corresponding regression functions on the basis of Snedecor *F*-test or Student *t*-test (Tables III, IV).

The group of species with small increments (0.05–0.20 mg f. wt per individual per day) can also be divided into two, univoltine and web spinning species displayed greater food demand than wandering and multivoltine species.

Laboratory and field estimates of the relation between consumption by individuals and body weight (Table V) were compared. The differences found depended on the food dosage. Feeding experiments, where a part of series was given insufficient food (less food than the average demand) corresponded better to field conditions than when there was given a food excess.

Analysed species of spiders displayed high flexibility as regards the amount of food consumed in relation to the food supply in the environment (Fig. 2). The consumption increased by several tens of times according to the increasing food supply. Even under conditions of food excess the consumption by an individual increased together with the number of prey supplied (Table VI, Fig. 2).

Most efficiently utilized (highest predation) was the food given in insufficient amounts (up to 0.05 mg/mg body weight of spider per day). Spiders consumed over 70% of the prey supplied (Fig. 3).

At increasing food doses the utilization of food gradually decreased and under conditions of most abundant feeding (over 1 mg/mg body weight of an individual) it was 6–28% (Table VI, Figs. 3, 4).

On the meadow *Stellario-Deschampsietum medioeuropaeum* most frequently caught by spiders were the dipterans of four families: Sciaridae, Cecidomyiidae, Bibionidae, Chironomidae (Kajak and Olechowicz 1969). The same families dominated also in the environment as regards the intensity of emergence (Olechowicz 1971). The number of dipterans caught by spiders was correlated with the intensity of emergence and not with their current biomass on the meadow (Table VII). This proves that the dipterans were caught effectively immediately after their emergence. Mean reduction of the number of emerging dipterans caused by three dominant web spinning species was 37%. The dipterans, belonging to four most commonly represented families, were reduced in 52%.

8. POLISH SUMMARY

Porównano funkcje regresji określające zależność między ciężarem ciała a konsumpcją pajaków. Funkcje wyznaczone na podstawie materiałów własnych, dotyczących gatunków *Araneus quadratus*, *Singa heri* i *Tibellus maritimus* (tab. I), lub na podstawie danych piśmiennictwa – *Linyphia triangularis* (Turnbull 1962), *Tarentula kochii* (Hagstrum 1970a), *Pardosa lugubris* (Edgar 1971) i *Trochosa ruricola* (Stejgwiłło-Laudańska 1971).

Stwierdzono, że grupa gatunków wyróżniająca się największym przyrostem ciężaru ciała (ponad 0.5 mg św. m. na osobnika przez dzień) odznacza się też większym zapotrzebowaniem pokarmowym (rys. 1, tab. II). Różnice są statystycznie istotne, co stwierdzono porównując odpowiednie krzywe regresji za pomocą testu *F* Snedecora, względnie testu *t* Studenta (tab. III, IV).

Grupa gatunków o małych przyrostach (0.05–0.20 mg św. m. na osobnika przez dzień) też może być podzielona na dwie: gatunki jednoroczne i sieciowe wykazywały większe zapotrzebowanie pokarmowe, niż gatunki wędrujące i wieloletnie.

Porównane zostały laboratoryjne i terenowe oceny wielkości konsumpcji osobników o określonym ciężarze (tab. V). Różnice otrzymanych wyników zależały od sposobu dawkowania pokarmu w hodowli. Hodowle, w których część serii karmiono niedostatecznie (dawki pokarmu mniejsze od przeciętnego zapotrzebowania), lepiej odpowiadały warunkom terenowym, niż hodowle karmione nadmiarem pokarmu.

Analizowane gatunki pajaków wykazywały wielką elastyczność jeśli chodzi o ilości zjedanego pokarmu, zależnie od wielkości bazy pokarmowej w środowisku (rys. 2). Przy dużym zróżnicowaniu bazy pokarmowej (niedostateczne karmienie pewnych hodowli a nadmierne innych) obserwowano kilkudziesięciokrotny wzrost konsumpcji.

Nawet w hodowlach utrzymywanych w warunkach nadmiaru pokarmu następowało zwiększenie konsumpcji osobnika w miarę powiększania liczby dostarczanych ofiar (tab. VI, rys. 2).

Najbardziej efektywnie (największa redukcja dostarczanych ofiar) był wykorzystywany pokarm dawkowany w niedomiarze (nie więcej niż 0.05 mg na mg ciężaru ciała pajaka na dzień). Pajaki zjadały ponad 70% dostarczanych ofiar (rys. 3).

W miarę zwiększania dawek pokarmu stopniowo zmniejszało się wykorzystanie pokarmu wynosząc w warunkach najbardziej obfitego karmienia (powyżej 1 mg na mg ciężaru ciała osobnika) od kilku do kilkunastu procent (tab. VI, rys. 3, 4).

Na łące *Stellario-Deschampsietum medioeuropaeum* najczęściej trafiają w sieci muchówki należące do czterech rodzin: *Sciaridae*, *Cecidomyiidae*, *Bibionidae*, *Chironomidae* (Kajak i Olechowicz 1969). Te same rodziny dominowały też w środowisku pod względem nasilenia wylotów (Olechowicz 1971). Liczba muchówek łowionych przez pajaki jest skorelowana z intensywnością wylotów, a nie z ich aktualną biomasą na łące (tab. VII). Świadczy to o efektywnym wyłapywaniu muchówek natychmiast po wylocie. Przeciętna redukcja muchówek, powodowana przez 3 dominujące gatunki sieciowe, wynosiła 37% muchówek wylatujących w danym środowisku. Muchówki należące do czterech najpospoliciej reprezentowanych rodzin były redukowane w 52%.

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