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SYNBIOLOGICAL STUDY OF THE LIZARD POPULATIONS OF SANDY GRASSLANDS

F. GYOVAI

Attila József University, Department of Zoology, Szeged

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Abstract

In the course of a two years' study, author processed data of 634 individuals of the 3 lizard species (*Lacerta taurica, L. agilis* and *L. viridis)* living on a sandy grassland. The density of the lizard population was 557 individuals per hectare. The migration of the juvenile *L. taurica* tended towards the surrounding grazed areas. The *L. taurica* population belongs to mortality type No. II. The main mortality factor is predation. The covering by vegetation segragetes *L. taurica* from the other two populations. The consequences regarding habitude of the morphological differences between the 3 species presumably act in the direction of a decrease in interspecific competition between the individuals more than 1-year-old. The lizards represent a biomass of 1725 g/ha at the sampling area. Their annual nutriment consumption is 1.3 g/m^2, 18% of the complete secondary consumption, and 8% of the primary consumers' production. The lizards play a significant role in the regulation of the *Coleoptera, Aranei* and *Orthoptera* populations.

Key-words: Lacertilia, density, migration, niche analysis, interspecific competition, aliment consumption, aliment composition

Introduction

Our Department has been carrying out complex ecological investigations on sandy grasslands in the model area of Bugacpuszta since 1976 (MÓCZÁR et al., 1980). In the course of these studies, an answer was sought to questions of production-biology and ecological regulation. In this biocenosis secondary consumer populations have a significant role from the viewpoint of material- and energy-circulation, as wall as regulation (GALLÉ, 1978, FARKAS, 1978, GYENES, 1982). The present study aimed at investigating certain ecological parameters of the *Lacerta* species, reaching significant density in that area, first of all L. taurica. The author's objective was dual, viz. (i) studies on the causal background of the space-time pattern in rescept of the lizard populations; (ii) approach to the regulatory role of the biocenoses. In the present paper my studies on the population structure, the interactions between lizard populations, the biomass, the aliment composition and the alimentary consumption are summarized.

Material and methods

The studies were performed in 1981 and 1982 from March till October in a 2.38 hectare model area located at Bugacpuszta in the Kiskunság National Park. The region is an inhomogeneous sandy grassland interspersed with small sand-hill ridges and wind-furrows, and bordered by a forest at the North-eastern side. Till 1976, the area was mildly utilized for grazing, then it was isolated from the neighbouring area, where grazing was continued. Consequently, the *Potentillo-Festucetum pseudovinae* association covering a great part of the area is turning into *Festucetum-vaginatae* associations at the sand-hill ridges, and into *Molinio-Salicetum rosmarinifoliae* associations at the wind-furrows, in the course of secondary succession. The detailed botanic, pedologic, and microclimatic characterization of the sandy grassland has mainly been comprised in the works of Körmöczi (1982a, 1982b, Körmöczi et al., 1981). I worked with manual catching in the area. Numbered aluminium boards were placed every 10 m, to mark the exact location coordinates of the catchings. Three lizard species live in the sandy grassland, namely, the *Lacerta taurica taurica* (Pallas), the *Lacerta agilis agilis* (Linnaeus), and the *Lacerta viridis viridis* (Laurenti). Animals were collected at about two-week intervals. The following data were recorded: the date and place (with meter accuracy) of catching, the species, the age and the sex of the individuals as determined according to Dely 1978. The body circumference and two body-lenght parameters viz. from the nasal tip to the cloaca orifice and from the nasal tip to the tail end, were recorded, each with mm accuracy. The second longitudinal parameter was omitted of the tail was broken or regenerated. The body weights were determined with the help of PESOLA type spring scales, with 0.1 g accuracy. The average vegetation covering the soil was estimated and the air temperature and the relative humidity (5 cm from the soil surface) were measured by a THERM 2246 type electric aspiration psychrometre.

The lizards were marked by cutting off toe phalanges in various combinations (Woodbury 1956, Blanchard and Finster, 1933, — a modified method). The density of the lizard populations was estimated by recapturing of labelled animals according to the method of Bailey's so-called triple-cath, based on Lincoln's index (Southwood, 1978). Samples were taken from a few stomach contents however, the catheter method (Opatrny 1980, Smith and Milstead, 1971. Legler and Sullivan, 1979) often failed, therefore, the material of the aliment analysis was mostly formed from the stomach content of the *L. taurica* individuals which perished in the glycol insect traps on the spot.

On the 47 days spent in the field I processed, the data for 484 *L. taurica*, 169 *L. agilis*, and 228 *L. viridis* specimens comprising the data for the recaptured individuals. Eleven *L. taurica* individuals different in age and sex were collected for laboratory studies concerning aliment consumption from the grass-plots in the neighbourhood of the area. The animals were kept in 30×40 cm sized terraira and were fed with *Galleria mellonella* larvae.

Results and Discussion

1. DEMOGRAPHIC PARAMETERS

1.1. Density

The density of *L. taurica* was found rather high: in yearly average 837±37 for the whole area (2,4 ha), i. e. 351 individuals per ha. The density was lower for *L. agilis* viz. 348±90/2.4 ha, i. e. 146/ha, and still lower for *L. viridis*, viz. 144±45/2.4, ha, i. e. 60/ha. The total density was 557 lizards per ha. This represents a biomass of 1725 g/ha, which significantly surpasses the density 700 g/ha reported by Tinkle 1972. On the contrary. the total density determined in the present study on the other hand, was by one order of magnitude lower than the average density reported by Schoener (0.97 individuals per m^2), which is probably the highest density measured for lizards so far (Schoener, 1980). It should be taken into account that Schoener studied *Anolis* lizards, which have smaller bodies, in a field where the maintaining capacity of the environment was considerably great.

1.2. Territorial behaviour and migration

The spatial structure of the lizard populations is fundamentally determined by their territorial behaviour. On the basis of the distances between the catching and recatching points, information could be obtained regarding the territory fidelity and the degree of migration of individual lizards. As shown in Table 1, the juvenile *L. tau-*

Table 1. Migration of the 3 lizard species

	L. taurica		*L. agilis*		*L. viridis*	
	juv.	ad.	juv.	ad.	juv.	ad.
$\bar{x}$ (meter) — Average of migration distance —	17.26	11.20	8.78	12.50	34.18	13.37
S (dispersion)	19.65	7.69	5.46	10.32	38.49	11.74
S^2 (variancy)	386.24	59.17	29.87	106.70	1481.00	137.98
$S/\bar{x}$	1.14	0.68	0.62	0.82	1.12	0.87
$S^2/\bar{x}$	22.36	5.28	3.40	8.53	43.34	10.31
n (number of individuals)	45	15	14	6	38	8
0–10 m (%)	64.44	46.66	64.28	50.00	52.63	37.50
11–20 m (%)	11.11	40.00	35.71	16.67	7.89	50.00
21 m<(%)	24.44	13.33	0	33.33	39.47	12.50
maximal distance	75	26	20	26	115	36

rica and *L. viridis* individuals are significantly different from the adults of the same species in respect of migration. For example, the juvenile *L. taurica* individuals have a higher average recapturing distance than the developed individuals, and their variance is also essentially higher. This latter is caused by the fact that the great majority of the individuals turned up again either within 10 m (64%), or more than 21 m (24%) apart. On the basis of the high ratio of the 0–10 m capturings, it can be assumed that the residence district of the juvenile individuals is small and that recapturings suprassing 21 m — the majority of which is between 40 and 70 m — indicate migrat-

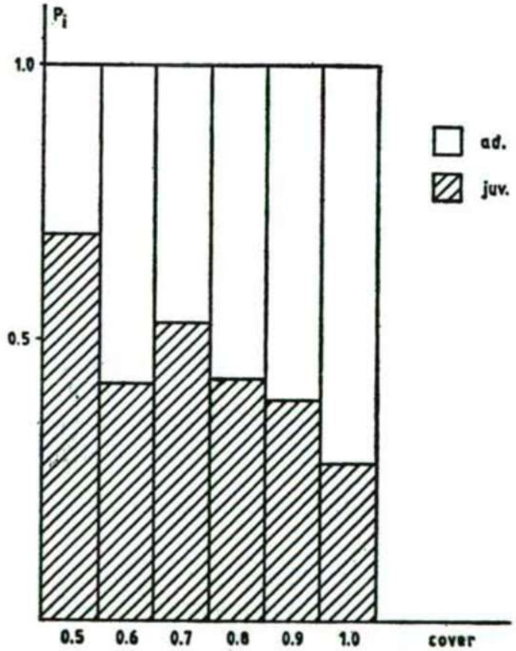

Fig. 1. Distribution of adult and juvenile individuals of *L. taurica* in the function of vegetation covering. P_i: relative frequency

ion. The adult *L. taurica* individuals appear in the 11–20 m recapturing category much more frequently (40%). The territories of these are presumably larger and less variable in size, and the migration is minimal. Presumably, the migration of the juvenile individuals supplanted from the network of the territories tended towards the surrouding grass-plots utilized for grazing where the density of the lizards is considerably lower (colonization for the occupation of "empty niche"-s (SCHOENER, 1968)). This means that juvenile lizards tending to avoid intra- and interspecific competitive effects become supplanted to areas with sparse vegetation (Fig. 1). Strong negative correlation was demonstrated between the ratio of the juvenile individuals and the covering vegetation:

$y=0.951–0.691x$
$r=-0.829 \qquad P<0{,}001$

(y = ratio of juvenile individuals, x-relative vegetation covering).
(r: correlation coefficient, P: significance).

The cause of the negative correlation may be attributed to that in the areas with higher covering, i. e. being more favourable for all three species, the juvenile *L. taurica* individuals do not tolerate the competition with *L. agilis* and *L. viridis,* and presumably predation in the case of L. viridis (WEBER, 1957, HOLEC and KMINIAK, 1970). Thus our model area, which is spared from grazing and treading functions as a pool for the *L. taurica* individuals and significantly promotes recolonization in the surrounding grass areas. All these support the view of our ecological team. This team had proposed to withdraw from grazing an area of 1–4 ha at the Bugac plain for protection of nature.

The data regarding the recapturing distances are in good agreement with the results of *Cruce* (1970). According to the present investigations, 64% of the juvenile L. taurica individuals were found within the area of 10 m diameter determined for this species on the basis of *Cruce*'s studies. For adults, *Cruce* found areas 15 m in diameter adequate. According to the present studies, 73% of the adult L. taurica individuals were refound within 15 m, and the farthest recapturing was only 26 m. These data speak against an exclusive protection of territories; they may overlap each other in this respect (RUBY, 1978). If the territory utilization were exclusive, there would be a need for about a 3-times greater area for an even space distribution of the more than 800 lizard individuals estimated in the model area. The migration of the juvenile *L. viridis* individuals showed even a higher frequency (39%). Their migration, however, did not tend towards the grazing pasture, but rather towards the neighbouring forest.

No significant age-dependence could be found for *L. agilis* individuals as to inclination to emigrate. Emigration of this species could not be demonstrated.

1.3. Age and weight structure, predational effect of the L. taurica population

The body weight and body length data for *L. taurica* individuals caught in 1982 were extrapolated to an arbitrarily chosen day (September 15, 1982), with the help of a growth curve drawn on the basis of experiences (Fig. 7). This method enabled us to study the *L. taurica* population at an exact point of time. The same could not be applied to the other two species, because the separation of the 1-year-old and older individuals encountered difficulties and the amount of samples was lower. Of the 324 *L. taurica* individuals studied by us: 185 were juvenile. 78 one year old, 45 two years old, and 16 three years old or older (Fig. 2). The equation of the continual straight line was as follows:

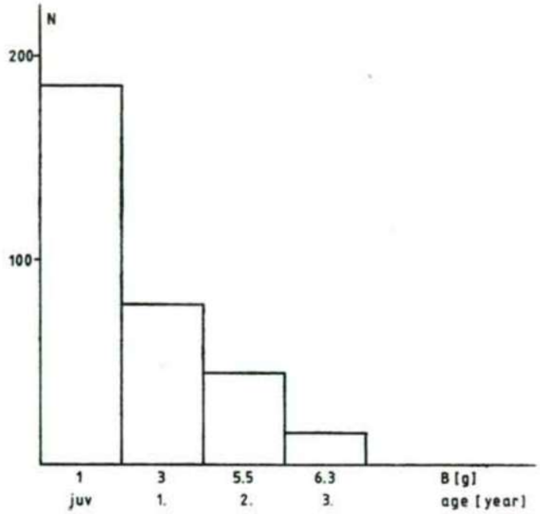

Fig. 2. Age- and weight-structure of *L. taurica* population. B(g): individual biomass, mean values expressed in grams; N: number of individuals

$$N = 216 - 54\,\mathrm{t} \qquad r = -0.94 \quad P \sim 0.05,$$

where N = individual number, t = age (in years).

In logarithmic form: $\ln N = 6.01 - 0.78\,\mathrm{t}$

$$r = -0.99 \qquad P < 0.02.$$

An average body mass value could be attached to each age group, therefore, the weight structure also analysed (Fig. 2). On the basis of the weight structure:

$$N = 242.88 - 34.65\,B$$
$$r = -0.95 \qquad P < 0.05$$
$$\ln N = 5.65 - 0.40\,B$$
$$r = -0.95 \qquad P < 0.05$$

(B = boby weight expressed in grams).

According to the mortality functions on the age and weight structure, it was justified to classify the studied *L. taurica* population into mortality type No. II, which means that the logarithm of the individual numbers shows linear decrease in the function of time. Presuming that predation plays a decisive part in the mortality of this population, I performed the following study. The frequency of broken tails is an indicator of predational pressure (TINKLE, 1972), therefore, the distribution within population of the total individuals belonging to the various weight groups (intact + regenerated + broken-tailed), and the lizards having intact tails were used in the χ^2 test (Table 2).

The assumption was therefore proved: close correlation was found between the rate of disappearance for the caught individuals, and the disappearance of lizards with intact tails. The potential predators of the lizards living in the model area are firstly birds *(Buteo, Falco, Corvus)*, perhaps mammals *(Insectivora, Mustelidae)*, and *L. viridis*.

Table 2. Ratio of the total to intact-tailed *L. taurica* individuals

Weight group (*g*)	p_i (total)	p_i (intact)
0.4–1.3	0.311	0.349
1.4–2.3	0.295	0.322
2.4–3.3	0.147	0.140
3.4–4.3	0.107	0.094
4.4–5.3	0.069	0.059
5.4–6.3	0.043	0.025
6.4–7.3	0.021	0.007
7.4–	0.002	0
	0.995	0.996

$\chi^2 = 0.0298$
$P > 0.99$

2. INTERACTIONS BETWEEN LIZARD POPULATIONS

The methods of niche analysis were used for the detailed studies on the environmental demands of the three lizard species. The justifiability of this is supported by PIANKA (1975), who pointed to the role of competition and niche relations in the organization of lizard communities. According to PIANKA and HUEY (1978), the microhabit and alimentary conditions may play a role in the niche segregation of lizards. This prompted me to study the factors determining the microhabit selection first of all. The analysis of the alimentary composition has already been performed for L. taurica.

2.1. Vegetation covering

It can be clearly seen in 3 that the vegetation covering shows irrelevant effect on *L. taurica,* while the other two species favour the regions of mass vegetation, mostly the wind-furrows. In accordance with this, the values of the niche overlapping regarding *L. taurica* are the lowest in the dimension of vegetation covering (Table 3, on the basis of the RENKONEN–SCHOENER formula). Also in conformity Fig. 3, the niche width values are the highest for *L. taurica* (Table 4). The niche centre of L. taurica is around 70% covering, in contrast to the 100% computed for the other two species. It is not the species composition of the vegetation which determines the choosing of living place, but rather the covering and structure.

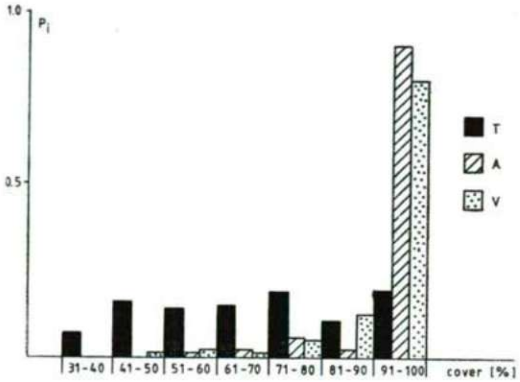

Fig. 3. Distribution of the 3 lizard species according to the vegetation covering. (T: *L. taurica*, A: *L. agilis*, V: *L. viridis*) P_i: relative frequency

Table 3. Niche overlapping of the 3 lizard species in the dimension of vegetation covering

	L. taurica	*L. agilis*	*L. viridis*
L. taurica	1		
L. agilis	0.278	1	
L. viridis	0.374	0.842	1

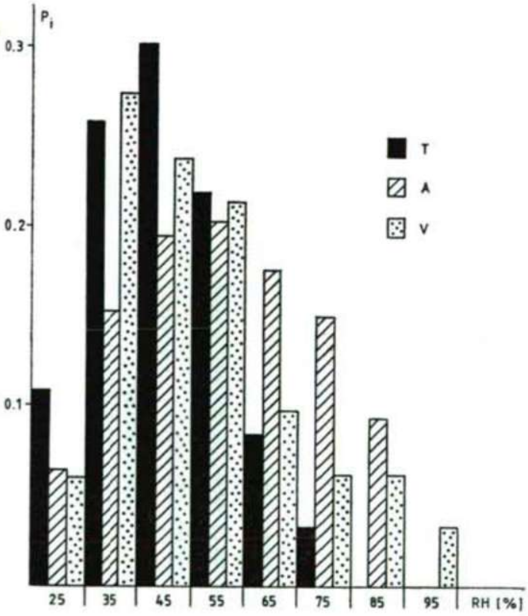

Fig. 4. Distribution of the 3 lizard species on the basis of relative humidity

2.2. Relative humidity

The histogram of this factor is illustrated in Fig. 4. The overlapping values between the three species are high in this dimension (Table 5). The niche centre for *L. taurica* is characterized by 47% relative humidity: for *L. agilis* and *L. viridis* the corresponding percentages are 56% and 51% respectively. There is no significant variation in niche width between the three species. Table 4 comprises the values of the niche width calculated by SHANNON's formula expressed in ln, regarding the three lizard species, in the studied three dimensions.

***Table** 5.* **Niche overlapping of the 3 lizard species on the basis of RH %**

	L. taurica	*L. agilis*	*L. viridis*
L. taurica	1		
L. agilis	0.694	1	
L. viridis	0.818	0.762	1

2.3. Temperature

The studies regarding air temperature do not show segregation of the three populations (Fig. 5, Table 4). (Here a role can be attributed to the colour and structure of the sand soil surface, due to the varying degree of reception of isolation). The niche centres per species, viz. *L. taurica:* 27.8 °C, *L. agilis:* 26,7 °C, *L. viridis:* 26.3 °C, show rather slight variations. Comparing these data with the relevant results of the studies accomplished by KORSÓS (1982a, b), the following determinations could be made regarding *L. agilis* and *L. viridis*. The niche width of these two species is closely similar to the niche width obtained in the present study, nevertheless, in the latter

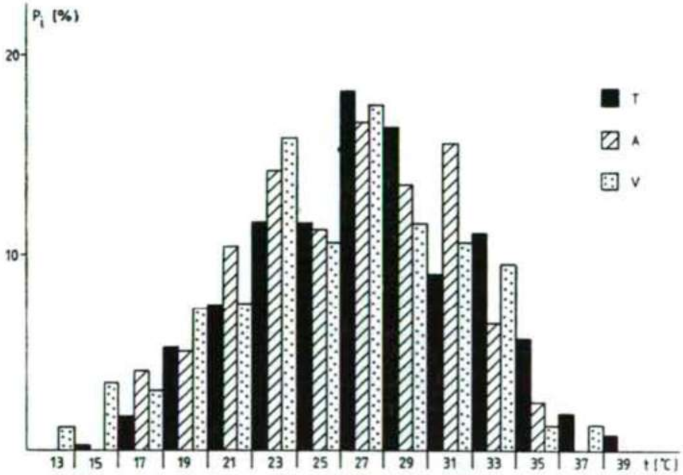

Fig. 5. Distribution of the 3 lizard species according to temperature

Table 4. Niche width values for the 3 lizard species in the three studied dimensions

	B%	RH%	t (°C)
L. taurica	3.17	2.27	2.24
L. agilis	0.44	2.49	2.16
L. viridis	0,72	2.43	2.28

case, a conspicuous shift towards higher temperatures was experienced (+10 °C for *L. agilis,* +4 °C for *L. viridis*). This might be attributed to the different character and climate, of the areas studied by us.

As shown by the studies on the three niche dimensions, the vegetation covering causes a very large segregation between the three populations. The lizards choosetheir place of living on the basis of the mass of the vegetation (SCHOENER, 1978).

2.4. Morphological differences

The morphological differences may have a potential role in the separation of species according to habit (KORSÓS, 1982b). Table 6 demonstrates the values of the two characteristic body ratios by species; namely, the tail length per body length (F/L) and body width per body length (K/L) ratios. In these studies each samples consisted of 30 individuals irrespective of age, fordoby ratios of did not distinguish juvenile lizards from developed ones. PLETICHA (1968) and KORSÓS (1981) found isometric postembryonal growth. The F/L constant for L. taurica and *L. agilis* can sharply be distinguished from the at for *L. viridis*. Due to its greater dispersion, the K/L ratio shows some difference — although not an unambiguous one — between sand lizard, and the other two species.

Table 6. Body ratio values for the 3 lizard species

	L. taurica	*L. agilis*	*L. viridis*
F/L	1.651	1.668	1.915
S (dispersion)	0.103	0.117	0.089
K/L	0.503	0.579	0.566
S (dispersion)	0.048	0.039	0.025
Morphological characterization	short-tailed slim	short-tailed squat	long-tailed squat

A close correlation has been demonstrated in respect to the lizard's jaw length and the size of the prey (KORSÓS, 1982b). I compared in this context the body length with the aliment proportions from the data pairs of 110 L. taurica and its prey. The relationship found between these can be demonstrated by the following function:

$$y = -3.84 + 0.22\,x$$

$$r = 0.570 \qquad P < 0.001$$

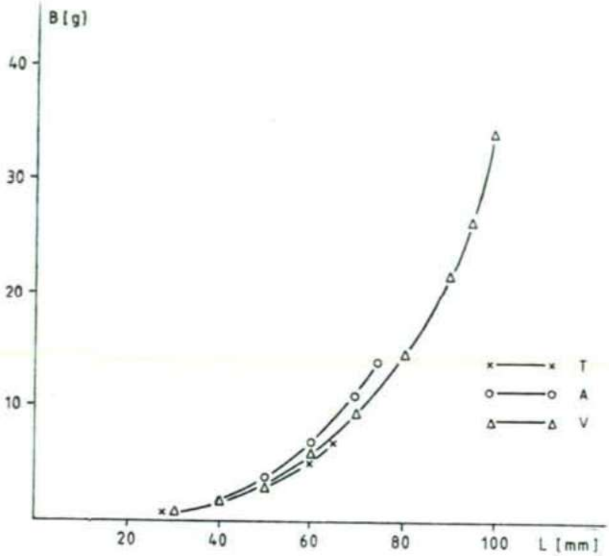

Fig. 6. Body length and weight curves for the 3 lizard species L: body length

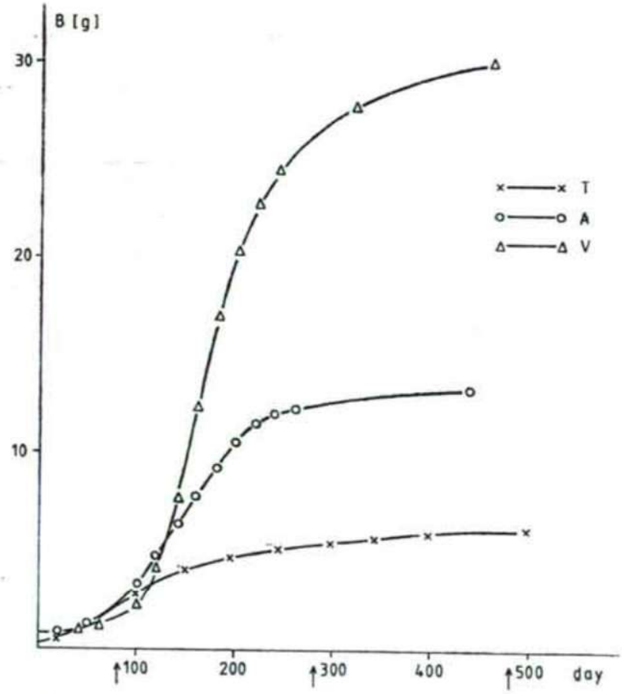

Fig. 7. Growth curves for the 3 lizard species (↑ =hibernation)

where y = dimension of prey in mm, X = the body length of *L. taurica* in mm. On the basis of the close correlation between the prey dimension and jaw length SCHOENER and GORMAN refer to relationships regarding competition (SCHOENER and GORMAN 1968). In respect of the evolution of the interspecies differences in body size DUNHAM and TINKLE 1978 also propound the role of competition.

Since the correlation shown in Fig. 6 exists between the body length and weight of the three lizard species, the measures of the prey can accordingly be examined in the function of body weight. It is striking in Fig. 6 that the curve of *L. agilis* runs above that of *L. viridis,* and the curve of *L. taurica* runs below it. Here I refer back to the K/L values and the morphological characteristics demonstrated in Table 6. Accordingly competition regarding aliment only exists between individuals of similar body weight. In this respect, therefore, interspecific competitive interaction can only be determined between juvenile individuals in autumn and spring. The reason for this is the different growth rate of the three species (Fig. 7). Following the spring of the first hibernation, the relative growth of all three species shows a strong outset (CRUCE, 1970, regarding *L. taurica*) (Fig. 8). Nevertheless, in respect of body weight and body length *L. agilis* strongly, and *L. viridis* rather intensely surpass *L. taurica.* It has been shown that in regard to the obtainment of food the 1-year-old or older lizards of varying species do not exclude each other competitively. If later on, certain degree of competition arises between them — interactions of growth curves — this is limited to a rather short period.

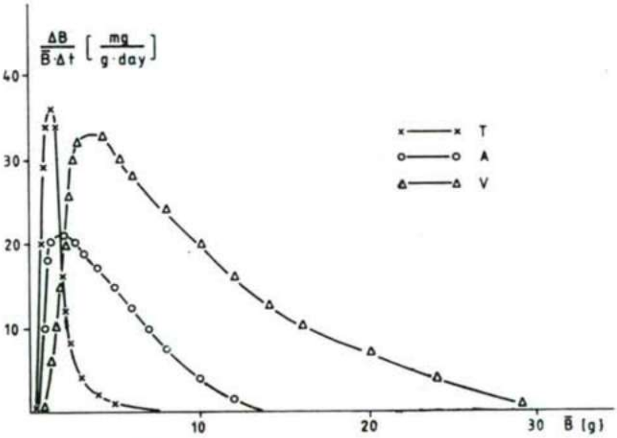

Fig. 8. Relative growth of the 3 lizard species

$\frac{\Delta B}{\overline{B}\cdot\Delta t}$: relative increase in body weight

3. THE PLACE OF LIZARDS IN THE ALIMENTARY NETWORK

3.1. Individual biomass changes and food consumption

Here the aim was not a detailed analysis of production-biology, but only the demonstration of the laboratory studies related to the food consumption of the characteristic lizard species of the model area, viz. *L. taurica.* Fig. 9 shows a correlation

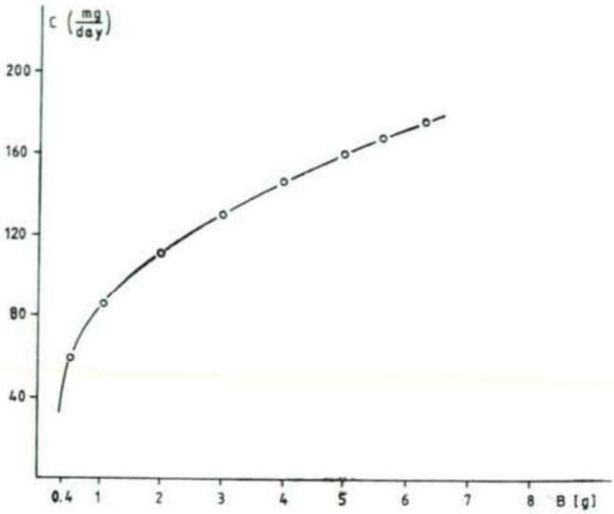

Fig. 9. Individual biomass changes and food consumption of *L. taurica*
C: aliment consumption (fresh weight mg per day)

between the changes in biomass and food consumption. With the *x–y* value pairs of this graph the following logarithmic function was obtained:

$$\ln C = 4.32 + 0.479 \ln B$$
$$r = 0.984 \qquad P < 0.001$$
$$C = 75.24\, B^{0.479}$$

B = live weight (gram)
C = food consumption (fresh weight mg per day)
C' = food consumption (dry weight mg per day) = 0.205 C

The function is in good agreement with the relevant results of the work of AVERY (1978), who author reported on the following relationship: at low temperature: $C' = 19.3\, B^{0.71}$, at high temperature: $C' = 34{,}6\, B^{0.65}$. Despite the similar course of our functions, the experienced variations were presumably caused by differences in the animals of alimentation as well as the studied objects (*Podarcis muralis* and *P. sicula*), since the average active body temperature of these species was 33.6 °C and 35.2 °C, respectively, i. e. about 8 °C higher than that in the case of the *L. taurica* regarding the present study. Thus, the food consumption of the *Podarcis* species is almost the double that of *L. taurica.*

In the knowledge of the weight structure, density and consumption of *L. taurica* population ,the biomass and average daily food consumption values of this species can be calculated for the model area. For the other two species the biomass and the aliment consumption values were estimated by extrapolation. The annual average biomass values were as follows:

$$B_{(L.\ taurica)} = 831 \text{ g/ha}$$
$$B_{(L.\ agilis)} = 584 \text{ g/ha}$$
$$B_{(L.\ viridis)} = 360 \text{ g/ha}$$
$$B_{(total)} = 1725 \text{ g/ha.}$$

In comparison with other studies, this is a rather high total biomass value. TINKLE (1972), e. g. reported 700 g/ha. Values of the daily food consumption:

$$\begin{array}{l} C_{(L.\ taurica)} = 36.1 \text{ g/ha} \cdot \text{day} \\ C_{(L.\ agilis)} \approx 20.4 \text{ g/ha} \cdot \text{day} \\ \underline{C_{(L.\ viridis)} \approx 10.2 \text{ g/ha} \cdot \text{day}} \\ C_{(total)} \approx 66.7 \text{ g/ha} \cdot \text{day.} \end{array}$$

The period of activity of the lizards can be estimated to 200 days per year, thus their annual consumption amounts to 1.334 g/m^2. Taking into account the consumption by the other carnivores living in the model area (firstly, *Aranei, Formicoidea*) we may state lizards take up 18% of the food amount flowing into the secondary consumption level, 8% of the production regarding the primary consumption level, and 0.66% of the primary production (FARKAS, 1978; GALLÉ, 1978, GYENES, 1982).

3.2. Qualitative composition of aliment

Table 7 summarizes the results of the analysis of the stomach content of 24 *L. taurica* individuals. Trophic levels: primary consumers (1), secondary consumers (2), decomposers (3), sustinents (4). Fig. 10 illustrates the percentual quota of the prey listed into the four trophic levels, regarding aliment.

The diversity value of the prey (SHANNON and WEAWER 1949) is the following: $H(S)=2.28$. The highest reachable value here would be $H(S)_{max}=2.89$.

$$\frac{H(S)}{H(S)_{max}} = 0.78$$

Table 7. Stomach content of 24 *L. taurica* individuals

Taxon	Trophic level	*n* (individual number)	%
Gastropoda	3	3	2.65
Collembola	3	7	6.19
larva (indet)	1	3	2.65
larva (indet)	2	1	0.88
larva (indet)	3	1	0.88
Blattidea	3	3	2.65
Mantidea	2	1	0.88
Orthoptera	1	11	9.73
Heteroptera	1	3	2.65
Homoptera	1	7	6.19
Neuroptera	2	2	1.77
Coleoptera	1	34	30.09
Coleoptera	2	0	0
Coleoptera	3	2	1.77
Lepidoptera	1	1	0.88
Diptera	3 and 4	3	2.65
Hymenoptera	4	1	0.88
Formica	2	9	7.96
Aranei	2	21	18.58
Total:		113	99.93

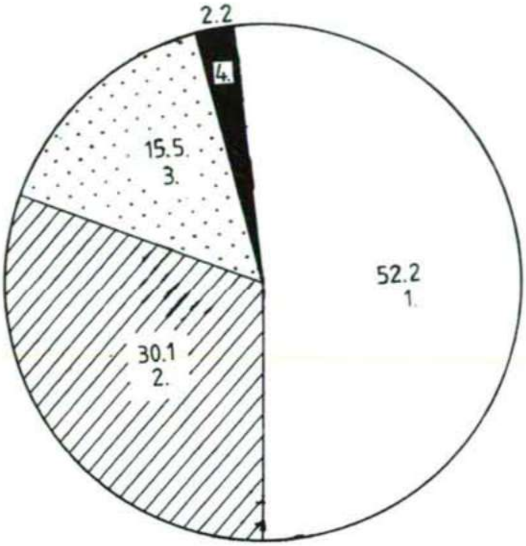

Fig. 10. Percentual composition of the aliment of *L. taurica*.
1: primary consumers, 2: secondary consumers, 3: decomposers, 4: sustinents

This means that the aliment composition of this species is variable. The diverse aliment composition and the specialization of low degree is presumably a general characteristic of *Lacertidae* (ROBINSON and CUNNINGHAM 1978). The above values were determined for relatively large taxonomic categories, lizards choose prey on the ground of the general appearance, motility and dwelling of the prey; and they do not take its species into account. Table 7 shows that insects flying well (for example *Diptera, Lepidoptera, Neuroptera,* etc.), that is, those difficult to catch represent a slight proportion of the in consumption. *L. taurica* may play a significant role in the control of phytophage beetles and spiders. According to BALLINGER (1979), in the periods abundant in nutriment lizards "change to" the consumption of aliments of larger bodies. It may be assumed, therefore that at the time of the mass increase of the Locusts, the lizards of Bugac also play a role in the regulation of these.

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Address of the author:
F. GYOVAI
Department of Zoology, A. J. University
H-6701 Szeged, P.O. Box 659.
Hungary