Comparative niche analysis of two sympatric lizard species (Lacerta viridis and Lacerta agilis)

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Abstract: A capture-mark-recapture investigation on two sympatric populations of Lacerta viridis and L. agilis has been carried out for a period of two years. Niche segregation has been studied from three main points of view: microhabitat, daily activity pattern and food selection. SCHOENER's measure of niche overlap was used in clarifying the roles of various factors. Food niche breadths of the two species has been described by an analysis of resource utilization curves. The following approximately equal in weight three factors are considered to be of greatest importance in the ecological segregation: 1. microclimatic and activity pattern differences, 2. prey taxa, and 3. prey size.

Coexistence of two closely related species populations may be preserved in the same biotope (in sensu UDVARDY 1959) for a long time only by niche segregation. Populations can reduce competition by partitioning the environmental resource set and by adapting to the conditional factors which regulate the utilization of these resources. In such a way similar species can live together permanently. Ecological studies on niche segregation are important not only for the knowledge of species coevolution but also in trying to save the endangered species from extinction.

In the present study I analyse the niche relations of sympatric Lacerta viridis and L. agilis populations. The first part of the results of the two-year investigation included a clarification of dispersion patterns, a morphometrical analysis and a preliminary comparison of niche dimensions (KORSÓS 1982). The purpose of the following part is to answer questions such as: Which are the niche factors principally responsible for the coexistence of the two lizard populations? What survival values do these populations occupy? To what extent do they overlap? How long can their coexistence be preserved?

Niche segregation has been studied from three main points of view (PIANKA 1973): habitat, time and food. Some authors (e.g. WEATHERLEY 1963) consider food segregation to be of such great importance that they think niche to be identical with the animals' functional status in the food web. Habitat partitioning is one of the most frequent studies of niche (SCHOENER 1968, ROSE 1976). Within it many variables can be selected (e.g. vegetational structure, temperature, soil types, etc.), partitioning of which among different species is usually measured (PIANKA & PIANKA 1976, SIMON 1976, SIMON & MIDDENDORF 1976). Although every species has its own habitat (UDVARDY 1959), in the case of these sympatric lizard species it is more correct to talk about mi-

crohabitat differences because of the close niche relations. Time as niche dimension may only crop up in connection with the animals' activity periods. Segregation of this regarded as occasional (SCHOENER 1974), but probably only little investigated. The relationship of the two lizard populations is presented according to these three main points of view.

MATERIALS AND METHODS

The study area, situated in the field site of the Game Biology Reserach Station of the University of Agriculture, Gödöllő, was characterized in detail in a previous paper (KORSÓS 1982). The methods of collecting data on the individually marked lizards were also described there. In addition to measurements of environmental variables (soil and air temperatures, intensity of light exposure, plant density, soil type, wind velocity) the food of the lizards has also been studied. The basis of this was the material of stomach contents collected by I. SZABÓ. Some head proportions suspected to be correlated with food size were also measured. These are length and width of pileus, head depth and snout-ear distance; all of them expressed in percentage of total snout-vent length. The specimens from which the stomach contents examined are deposited in the Zoological Department of the Hungarian Natural History Museum.

Niche overlap was measured according to SCHOENER (1968). That means graphically the common area under the curves of relative frequency distributions describing the demands of the two species. Mathematically:

$$1 - \frac{1}{2} \sum_{i=1}^{s} |p_{xi} - p_{yi}|$$

where p_{xi} and p_{yi} are the relative frequencies of the two species (x and y) belonging to the i-th category of the resource set (s). SCHOENER's formula has a great adventage over that of LEVINS (1968), namely that its extreme values are 0 and 1, and it is equal for both species (i.e. symmetrical).

In the case of microclimatic variables the overlap was calculated on the basis of extreme, limiting values. This, being asymmetrical to the species is actually rather similar to the competition coefficients, but the three-dimensional representation of niche would have demanded a more difficult method to obtain a symmetrical formula.

In some cases (calculating the overlap of the microclimatic variables, head measurements of the lizards, and the microhabitats and activity periods together) discriminant analyses were performed on an IBM 3031 computer using the BMDP statistical package (DIXON 1981). The option for reclassifying every case to one of the two groups according to the classification function obtained in the analysis results in a probability of misclassification, which may also be considered as a measure of niche overlap (STEINHORST 1979).

RESULTS

Sample data are listed in Table 1. The data recorded in the study area include not only the handled but the sighted and identified lizards as well. The population sizes, estimated by the computer programme of OTIS et al. (1978) have been found as 48 ± 9 for L. viridis and 96 ± 15 for L. agilis. The population densities (80/ha and 160/ha, respectively) are in accord with those of PETERS (1970) and TERTISHNIKOV (1970).

It was possible to reduce the soil and air temperature and the measurement of light exposure out of the environmental variables on the basis of a principal component analysis detailed elsewhere (KORSÓS 1982). They affect niche segregation in a way similar to one another acting as microclimatic variables. The positive correlation between them also supports this relationship ($x^2 = 30.58$; $p < 0.1$ %). The volumes fit for survival of the populations are delimited by the extreme-limit values of the three variables as shown in Fig. 1. L. viridis has a restricted activity as regards air temperature and light exposure as well, but it definitely shows preference for warmer values of soil temperature. L. agilis has generally a greater tolerance, however it does not favour higher soil temperature. The overlaps calculated from the limiting values are 64.9 % for L. viridis and 31.2 % for L. agilis. Regarding not only the extreme positions of the survival volumes, but the relative frequency distributions of discriminant scores of the microclimatic variables, the overlap between the two species has been found as 63.5 %.

Table 1. Number of lizard specimens observed, captured or taken into the various analyses

Species	Year	Number of observed specimens	marked specimens	Recaptures pc.	Recaptures %	microclimatic variables	soil types	vegetational categories	wind velocity	activity periods spring	activity periods summer	stomach contents
Lacerta viridis	1980	44	28	3	10.7	-	44	44	-	19	24	-
	1981	38	18	5	27.8	19	38	38	38	10	27	-
	total	82	46	8	17.4	19	82	82	38	29	51	16
Lacerta agilis	1980	35	27	5	18.5	-	35	35	-	22	13	-
	1981	45	31	12	38.7	27	45	45	45	27	18	-
	total	80	58	17	29.3	27	80	80	45	49	31	21

Determining the proportion of soil particles smaller than 0.002 mm in the samples (i.e. clay) we can obtain information on the mechanical composition or physical properties of the soil types. In the study area the clay content was between 21.20 - 34.44 %. This refers uniformly to adobe - clayey adobe texture. Comparing the soil samples to the capture points of the lizards (i.e. determining whether the populations are distinguishable or not only on the basis of the soil texture where they occur), the relative frequency distributions coincide almost completely. The value of overlap is 91 %.
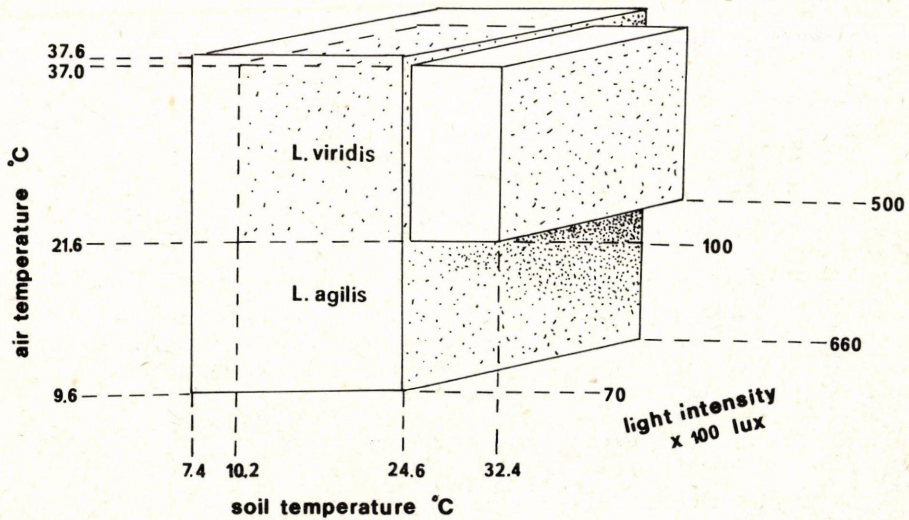

Fig. 1. Niche volumes of the two species bordered by the microclimatic variables

According to the woody vegetational categories (KORSÓS 1982) the lizards are distributed as in Fig. 2. There is a mild tendency of L. viridis to occur at higher values (i.e. in denser and loftier woods and shrubs) with greater relative frequency, nevertheless the calculated overlap between the two species has been found as high as 74.1 %. Testing the distributions of woody vegetation and capture points of lizards I found no significant interrelationship between them (X^2 = 21.84; p > 30 %).
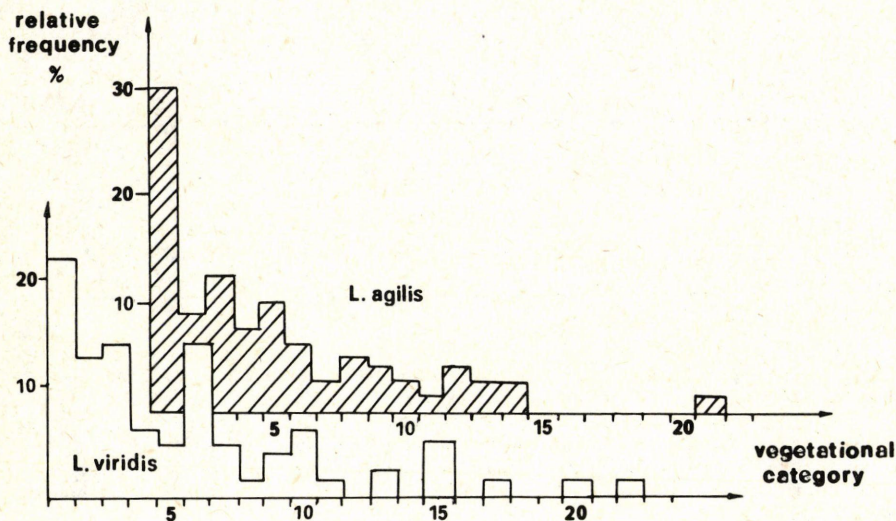

Fig. 2. Relative frequency distributions of lizards according to ligneous vegetational categories

Examination of changes in the number of lizards observed and in the average wind velocity data together was aimed at the differences in activities of the two species on variously windy days. The data and the correlation matrix (Table 2) show that the lizards were active (catchable) independently of the velocity of the wind.

Table 2. Correlation matrix of changes in lizard activities and wind velocity data

	Lacerta viridis	Lacerta agilis	wind velocity
Lacerta viridis	1		
Lacerta agilis	0.4953	1	
wind velocity	0.0656	0.1640	1

In addition to the above treated spatial niche segregation there is another possibility for durable coexistence of two populations: temporal resource partitioning (PIANKA 1973). This niche dimension actually means periods of foraging or other activities. The overlap of utilization functions of limited environmental resources may be reduced to a high degree with the temporal separation of utilizations (e.g. diurnal and nocturnal foraging strategies). However, neither of the sympatric populations of L. viridis and L. agilis can realize nocturnal activity because of the substantial fall of temperature during the nights in the temperate zone, but they can effectively reduce competition by shifting their diurnal foraging periods.

It was possible to compile a spring and a summer activity diagram from the pooled data of the two-year investigation (Fig. 3). The overlap between the spring activity periods is 69 %. In this aspect the one-peak activity of the sand lizard and its earlier appearance in the morning are remarkable. The green lizard begins its foraging afterwards with a little fluctuation at high noon,

and it continues further in the afternoon. The overlap between the summer activity periods is 59.3 %. The situation is similar to that in the spring, but shifted a little earlier section of the day. The activity periods of the green lizard shows an interesting trimodal shape to be discussed later.
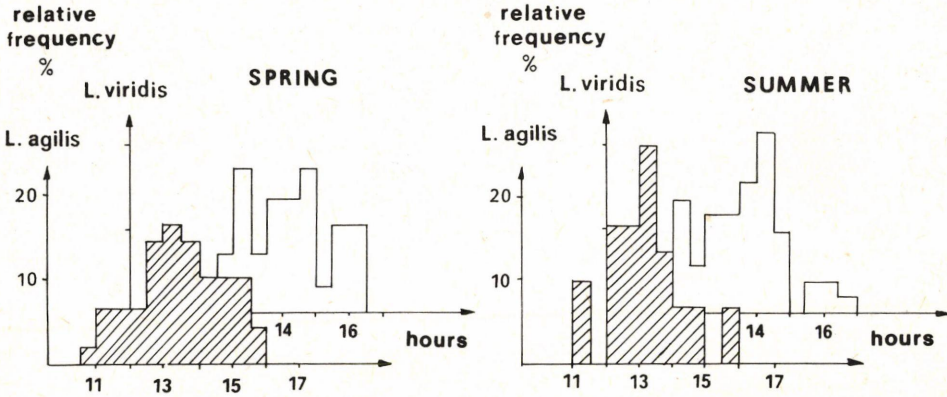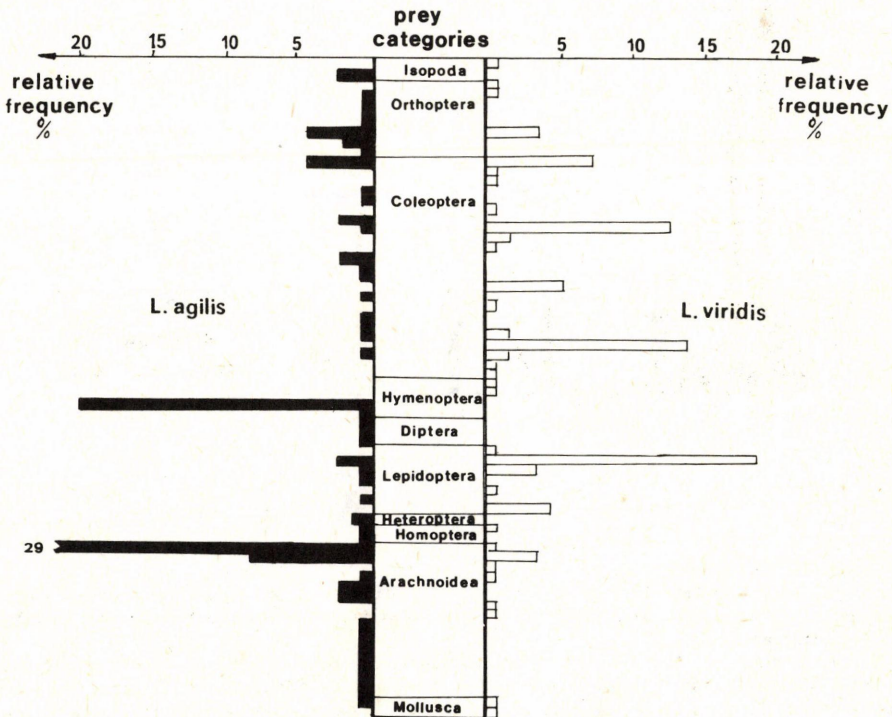

Fig. 3. Daily activity diagrams of lizards

Fig. 4. Food composition of lizards according to the prey taxa

The third and perhaps most important factor allowing coexistence is the sharing of food. The two mainly insectivorous lizard species have apparently very similar prey base (Coleoptera, Orthoptera, Lepidoptera larvae, Arachnoidea), but they differ with respect to species and sizes. Such a segregation may only be clarified by stomach content analyses. However, these studies are usually limited to small sample sizes (20-50 specimens) because of the methodological difficulties and the drastic interference with the native populations, especially in the case of lizards (SMITH & MIL- STEAD 1971, VERON 1969). The identification of the partly digested preys may also be rarely carried out to taxa lower than families.

With respect to taxonomic composition there are 12 common food categories of the two species. These are usually various genera of mainly Insecta and Arachnoidea. Diversity of stomach contents has been calculated according to SIMPSON (1949): L. viridis 0.088, L. agilis 0.141.

The weighted frequency distributions of the prey groups are shown in Fig. 4. The overlap of the 68 distinct categories is only 18.5 %. While the sand lizard has a greater Orthoptera, Diptera and Arachnoidea consumption, the green lizard selects more of caterpillars and beetles like Carabus or Cetonia. The latter preys however, lead us to the problem of food size segregation.
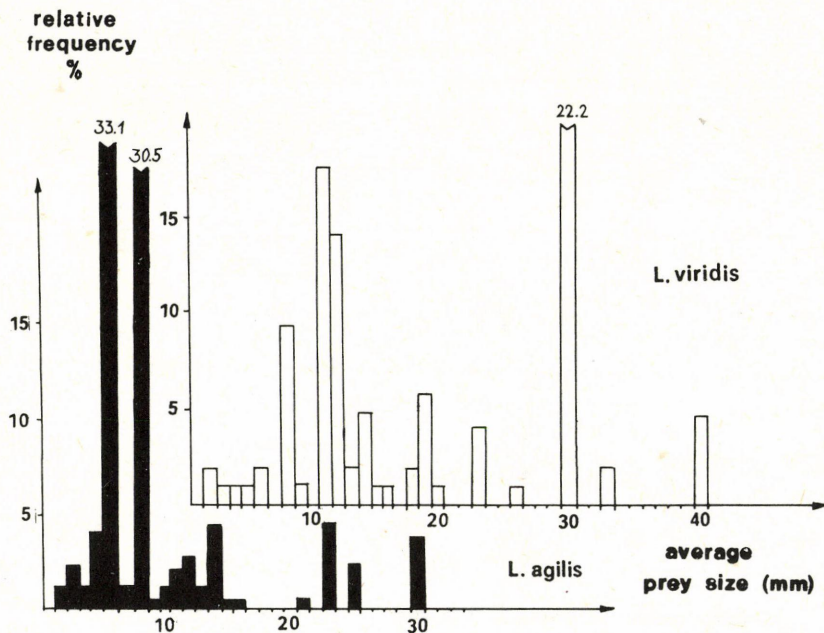

Fig. 5. Food composition of lizards according to the prey size

The frequency distributions in Fig. 5 have been obtained by pooling the prey groups with e- qual average body length. The overlap between the food sizes taken by the two lizard populations has been found as 35.2 %.

On the specimens from which the stomach contents had been analysed, four head measurements were taken. These were suspected to be correlated with the size of prey consumed. A discriminant analysis on the four variables has completely separated the two populations: the overlap (i.e., probability of misclassification) was equal to 0 (Fig. 6).

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On the basis of a resource utilization function of the food size as a niche dimension we can obtain information about niche width of a species (ROUGHGARDEN 1974). From data on average prey sizes, their frequency distributions and variances, and on the snout-ear distances of adult sand and green lizards the following niche widths have been calculated:

	total niche width	within phenotype component	between ph.comp.	niche position
L. viridis	60.0	96.8 %	3.2 %	14.3 mm
L. agilis	67.8	78.5 %	21.5 %	11.8 mm

In both species individual variability accounted for the greater part of total variance (see Discussion). That means that the animals are rather generalists with respect to food size.
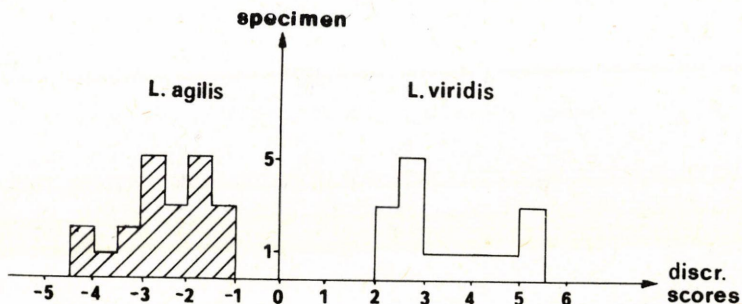

Fig. 6. Frequency distributions of discriminant scores of lizard head measurements

DISCUSSION

Differential adaptation to temperature and light conditions plays an important role in the microdistribution of poikilotherm lizards. The populations with different tolerance aspects maintain different relationships with the environmental factors affecting them. This situation is manifested in the geographical distribution of the two species as well. L. agilis is widespread through nearly the whole of the Palaearctic between the 40th and 60th degrees of latitude, but the other species shows greater preference for warmth. It occurs only south of the 52th degree of latitude. The other closely related species (L. trilineata, L. lepida, L. schreiberi) occur mostly in the Mediterranaeum (ARNOLD et al. 1978). Accordingly, L. viridis prefers higher soil temperature, as contrasted with L. agilis, which has a greater tolerance for variation in air temperature and light intensity. Since the two lizard populations have a common biotope in the study area, they cannot segregate by partitioning the given microclimatic conditions. but they can optimize their coexistence by utilizing different periods of the day and the whatever vegetational microheterogeneity there is.

According to some authors (VASVÁRI 1927, ARNOLD et al. 1978) it is presumable that the green lizards would prefer microhabitats with dense woody and bushy vegetation. A hypothesis that this microhabitat selection could be detected by examining the dispersion pattern of the green lizard population in comparison with that of the vegetation, had arisen previously (KORSÓS 1982).The results clearly show that there is no significant difference between the vegetation requirements of the two species. However, in Fig. 7 we can see another possible interpretation. In summer days the green lizards spend the disadvantageously sunny and warm hours of high noon in the shadow of bushes and shrubs. Thus the relative frequency of L. viridis specimens observed in dense woody vegetation increases and at the same time their occurrence decreases in the open microhabitats.

In the earlier or later parts of the day with more favourable temperature conditions in the open areas the situation is quite opposite. This behaviour is due to the lack of complementary tolerance aspect of the population, i.e. the active regulation of body temperature, which would be the direct answer to the exterior effects of the ambient temperature. A similar relationship has been described by OUBOTER (1981) for L. sicula salffi. Hence Fig. 7 may actually be interpreted as a niche response surface of L. viridis (MAGUIRE 1973), which reflects its population reply to the constant vegetation density and the changing temperature as environmental factors.

The physical structure of the soil and the velocity of the wind was found to have no distinct effect on the two lizard populations. The lizards occur frequently on soil types with 27-29 % of clay content, obviously because this is the most recurrent soil type in the study area. Hence the lizard populations seem not to make distinction between the soil types.

Differentiation in activity periods has already been observed in terrarium by SAINT GIRONS (1976). The less rigorous requirement of L. agilis for air temperature enables it to begin foraging earlier, but on the other hand the intolerance of high soil temperature forces it to finish it sooner. The strange trimodal activity curve of L. viridis requires further studies, but the functions itself is not unknown in bimodal form (for L. taurica, CRUCE 1970). For a possible explanation, let us compare the shapes of the activity diagrams of the two species around 13.00 hrs (Fig. 3). We can see an opposite situation: while the sand lizard has an activity maximum then, the foraging activity of the green lizard declines abruptly. In accordance with SCHOENER's hypothesis, temporal resource partitioning is determined by an energy balance (SCHOENER 1974). The question is whether the energy gained while feeding exceeds the sum of energy lost in foraging plus in the inactive periods, or not. If the answer is positive then the animal will be active and forage for food; if negative then the lizard will wait at rest. In our case, after increase in activity of the sand lizard it would not be worth for the green lizard to forage since it could not get enough prey, and so its loss of energy would be greater than the gain from the food. When the sand lizard retires because of the high soil temperature the green lizard may become active again, thus increasing its competitive ability.
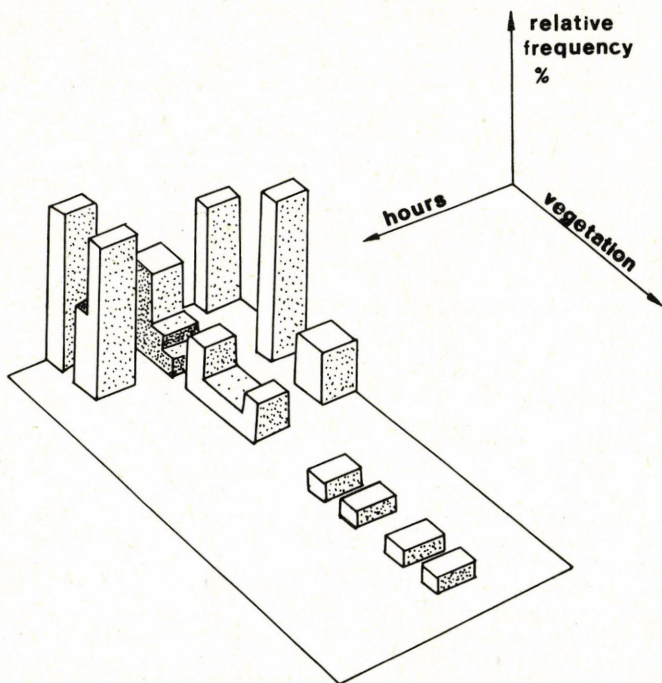

Fig. 7. Niche response surface of Lacerta viridis

Turning to the probably most important distinctive factor, the food, we can establish that though L. agilis has a broader prey spectrum, yet its trophic diversity (i.e., selectivity) is smaller (SIMPSON's formula has greater value at lower diversity!). It consumes more food categories (47) and makes little distinction among them. L. viridis is much more specialized in the quality of food, a notion which is supported by the low overlap value (18.5 %). Average prey size is also a considerable factor (35.2 %) as a consequence of the different body sizes of the species. Head measurements are generally accepted to be in good correlation with food size (SCHOENER 1968, SCHOENER & GORMAN 1968).

On the basis of ROUGHGARDEN's theory (1974), the total niche width of a population is equal to the variance of the probability density function of resource utilization, regarding in this case only food size as a niche dimension. Total niche width includes two components: the within phenotype component equals the variance of the resource utilization function of the individual, and the between phenotype component which is the same for the whole population. The former gives information on whether the population is composed of food generalists or specialists, and from the latter we can obtain evidence of the intensity of intrapopulation (interphenotypic) competition. According to the data (see Results), in the L. viridis population a strong interphenotypic competition dominates (small BPC variance). That may be connected with the elaborate social organization (frequent interactions, hierarchical fights) of green lizard population (WEBER 1957). Sand lizards show no such features (SCHULZ 1972).

From the analysis of niche segregation I have concluded that the three main dividing dimensions (habitat, time, food) of PIANKA (1973) are characters of unequal weight. Hence the factors affecting the resource partitioning of the populations were abstracted along the following three axes: 1. microhabitat (soil and air temperatures, light intensity, structure of vegetation) and activity periods; 2. food quality; 3. food size.

The allocation of food to two axes is justified by its important separating effect, indicated by the smallest overlap values: 18.5 and 35.2 %, respectively. The reduction of the other factors to one axis is also logical; thus their overlap value, calculated on the basis of a discriminant analysis, is only 39.7 %.

Connexion of the apparently independent dimensions (habitat and activity periods) in the first axis is not surprising. PIANKA's distinction inplies in reality a grave conflict. Time itself must not be taken as a niche dimension or environmental factor, because it is impossible to conceive a population tolerance aspect which is in direct complementary relation with time. Time is, similarly to chance, an inherent character of all environmental variables by virtue of their dynamical changes. Thus activity period may only be explained as a response of the population to some kinds of environmental factors. Air and soil temperatures are of this sort, and their dynamics is followed by the frequency distribution of active lizards as a population reply.

Environmental factors, ordinated along three main axes as detailed above, reduce to the minimal the overlap between the realized niches of the two populations. These realized niche volumes are not simply parts of the n-dimensional hyperspace, but actually its subspaces, because the seven factors observed in this study do not represent all the relevant conditions which may affect the populations.

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